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The Influence of Metacommunity Size on Species Diversity across Spatial Scales

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Division of Biology and Biomedical Sciences

Evolution, Ecology, and Population Biology

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The Influence of Metacommunity Size on Species Diversity across Spatial Scales

by

Lauren Michelle Woods

A dissertation presented to the
Graduate School of Arts and Sciences
Of Washington University in
partial fulfillment of the
requirements for the degree
of Doctor of Philosophy

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Dedication:

I dedicate this dissertation to my family who have supported and encouraged me through all of my endeavors, including this one.

ABSTRACT OF THE DISSERTATION

The Influence of Metacommunity Size on Species Diversity across Spatial Scales

by

Lauren Michelle Woods

Doctor of Philosophy in Biology and Biomedical Sciences

Evolution, Ecology and Population Biology

Washington University in St. Louis, 2014

Professor Tiffany Knight, Chair

This dissertation explores the influence of metacommunity size and landscape level processes, such as dispersal, on species diversity. A metacommunity is a group of local communities, or patches, connected by dispersal, and metacommunity size can be defined as the number of discrete local patches within a metacommunity. In chapter 1, I developed a framework to predict the effects of habitat destruction, or a reduction in metacommunity size, on the species richness of local patches of different sizes by integrating metacommunity theory with the equilibrium theory of island biogeography.

The effect of metacommunity size on species richness in small and large patches within a metacommunity depends on whether immigration rates or extinction rates are more affected by metacommunity size. Immigration effects result in a lower turnover in species between small and large patches with increasing metacommunity size, while extinction effects cause a higher turnover in species between small and large patches with increasing metacommunity size. The results of this model have implications for the effect of habitat destruction, or a reduction in

metacommunity size, on species richness in both small and large patches within a metacommunity.

In Chapter 2, I examined the effect of metacommunity size on species richness at local and regional spatial scales using a field survey of zooplankton species in replicate pond metacommunities. I found that metacommunity size has scale-dependent effects on zooplankton species richness. As the number of ponds in a metacommunity increase, the species richness of local ponds increases, but there is no change in richness at the regional spatial scale due to decreases in the turnover of species among communities.

The results of this study provide one of the first examples of species richness patterns changing with metacommunity size in a non-experimental system. In Chapter 3, I conducted an experiment investigating the effect of a natural drought disturbance on species richness in aquatic plant communities, and the importance of dispersal for the recovery of species richness.

I found that local species richness decreased in response to drought, and communities became more similar in their species composition. Species richness in communities with increased amounts of dispersal recovered to their pre drought conditions, suggesting that even low amounts of species dispersal can facilitate the recovery of species richness in aquatic plant communities.

In summary, this dissertation demonstrates that metacommunity size can affect species diversity, and highlights the importance of considering how landscape processes, such as dispersal, can influence the recovery and maintenance of species diversity.

Introduction

Species richness in individual communities and across a landscape results from the interplay between processes and dynamics occurring at both local and regional spatial scales (Ricklefs 2004, Leibold et al. 2004, Harrison and Cornell 2008). Metacommunity theory explicitly considers the interaction between local and regional scales (Leibold et al. 2004, Holyoak et al. 2005), providing a useful framework for understanding the partitioning of species richness across spatial scales. A metacommunity is defined as a group of local communities, or patches, connected by dispersal (Wilson 1992), and the number of discrete local patches defines the size of a metacommunity. Metacommunity size may be important for patterns of species richness at local and regional spatial scales, but its effects on metacommunity richness are just beginning to be explored (Munguia and Miller 2008, LeCraw et al. 2014).

One method for describing patterns of species richness, in particular the scaling of species richness with area, is using the species area relationship (SAR). The SAR is among the most well known phenomena in ecology, and describes the general relationship between habitat area and the number of species sampled (MacArthur & Wilson 1967, Schoener 1976, Connor and McCoy 1979, Lomolino 2000, Drakare et al. 2006). The most common model formulation of the positive relationship between area and species richness is the power law formulation, $S = CA^z$, where S and A are species richness and area, respectively, and C and z are curve-fitting parameters (Arrhenius 1921, He and Legendre 1996). This equation can be log-transformed to take on the linear form, $\log S = \log C + z \log A$, where z describes the rate of accumulation of species, or species turnover, with increasing area.

Although the SAR describes a simple and general pattern, the relationship between species and area can be described many different ways. According to Scheiner (2003), there are six different types of species-area relationships that can be defined depending on the type of sampling scheme and analysis used. In chapter 1 of this dissertation, I calculate a SAR as a curve produced from two ‘isolates’ (Preston 1962), or a type IV curve (Scheiner 2003) calculated from different sized islands (i.e. patches). The type IV curve is most often associated with the SAR of oceanic islands due to its promotion by MacArthur and Wilson (1967) (Scheiner 2003). When I calculate a z value between small and large patches in chapter 1, I am comparing the turnover in species richness between two habitats of different areas. However, in chapter 2 I measure the SAR as an accumulation of species across five sampled ponds. In this case, the SAR is calculated from non-contiguous habitat and Scheiner (2003) would consider it a type III curve. The z value obtained from the pond SAR is an averaging of the differentiation in species composition between ponds, since the order in which ponds are sampled to calculate z is randomized and repeated a number of times to obtain an average z . SARs can be calculated several different ways that are not considered in this dissertation, including using continuous habitats that are either nested quadrats (type I curve, e.g. Storch et al. 2012) or quadrats arranged in a continuous grid (type II curve, e.g. He and Hubbell 2011). All of these SARs describe the pattern of increasing species with area, but the interpretation varies for each one depending on the sampling scheme and analysis used.

In addition to measuring the relationship between increasing species richness with increased area, the SAR has also been used to make predictions about the impact of

habitat destruction on species loss (Pimm and Askins 1995, Brooks et al. 1999). In using the SAR as a tool for measuring habitat loss, many researchers have only considered going from one large continuous habitat, to a smaller, but still continuous habitat. However, habitat destruction often results in a loss of total habitat area and fragmentation (Fahrig 2003). In chapter 1, I develop a framework to predict the effects of habitat destruction, which occurs through the removal of habitat fragments, or patches, in fragmented landscapes, on local patch species richness by integrating metacommunity theory with the equilibrium theory of island biogeography (ETIB) (MacArthur and Wilson 1967). Metacommunity size is incorporated into the ETIB through decreasing patch extinction rates through rescue effects (Brown and Kodric-Brown 1977) or increasing patch immigration rates through the target effect (Gilpin and Diamond 1976) with increasing metacommunity size. I then compare how species richness changes in small and large patches located within different sized metacommunities. I also measure how the scaling of species richness, z , between the small and large patches changes with metacommunity size. This model provides new insights into the effect of habitat destruction, or a reduction in metacommunity size, on species richness in both small and large patches within a metacommunity.

In Chapter 2, I examine the influence of metacommunity size on species richness in a naturalized ecosystem. Metacommunity size might influence species richness at a regional scale by simply having more area to support more species (Connor and McCoy 1979), and influence species richness in a local patch by altering dispersal rates among patches within the metacommunity (Mouquet and Loreau 2003). Our current understanding on how metacommunity size affects patterns of species richness has come

from experimental manipulations (Munguia and Miller 2008, LeCraw et al. 2014), but no researchers have investigated these patterns in naturally occurring metacommunities. I conducted a large-scale survey of fishless ponds in Missouri in order to investigate the influence of metacommunity size on species richness at different spatial scales. I sampled zooplankton species richness of 62 ponds from 11 different replicate metacommunities that varied in metacommunity size (i.e. the number of ponds they contained). Freshwater ponds are an excellent system for studying metacommunity dynamics because of the discrete nature of aquatic habitats embedded within an uninhabitable terrestrial matrix (Cottenie et al. 2003). Additionally, zooplankton disperse readily between ponds via animals and wind in a mostly random fashion (Maguire 1959, 1963, Jenkins and Buikema 1998, Allen 2007, Frisch et al. 2012), making them ideal organisms for studying metacommunity dynamics. This represents one of the first attempts to document the influence of metacommunity size on species richness patterns in a non-experimental system

In the first two chapters of this dissertation I explicitly consider metacommunity size and how it might affect species richness. One of the main processes by which metacommunity size might alter species richness is through its effects on species' dispersal rates. In communities that are subjected to a disturbance, the size of the metacommunity it resides in might influence the recovery of species richness, since recovery processes are dependent upon a supply of propagules (Keller et al. 2002, Derry and Arnott 2007). For instance, Vellend (2003) found that the recovery of forest herb species richness in secondary growth forests was strongly influenced by the amount of surrounding 'ancient' forest, which served as a source of propagules.

In chapter 3, I do not directly manipulate metacommunity size, however I examine the influence of dispersal on the recovery of species richness following a natural disturbance. Natural disturbances play an important role in altering and maintaining patterns of species richness (e.g. Connell 1978, Sousa 1979). However, the frequency and intensity of these disturbances is expected to increase with climate change (Mitchell et al. 2006), which may lead to increasing species loss across ecosystems (Sala et al. 2000). Disturbances can affect ecological communities through stochastic processes, such as random species extinction (Hubbell 2001), or deterministic processes including species' niche interactions with changing environmental conditions (Chase 2007). The degree to which a disturbance acts stochastically or deterministically can result in different changes in species composition and species richness at local and regional scales. I examined the effect of a natural drought disturbance on species richness in aquatic plant communities, and I used a null modeling approach to analyze the relative stochastic or deterministic effect of drought on aquatic plant species. I also investigated whether varying amounts or timing of dispersal influences the recovery of aquatic plant communities following the natural drought disturbance.

Through a combination of theory, field surveys, and experiments, this dissertation demonstrates that metacommunity size can affect species richness, and highlights the importance of considering how landscape processes, such as dispersal, can influence the recovery and maintenance of species richness. Overall, this research contributes to a better understanding of the effect of metacommunity size on species richness at a local and landscape level, which can help provide insight into the potential effects of habitat loss and fragmentation on species richness at different spatial scales.

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Chapter 1

A metacommunity approach to modeling the effects of habitat destruction on species richness

Abstract

Habitat destruction results in a loss of total habitat area and fragmentation, and is a major cause of species extinctions. Despite the threat habitat destruction poses to biodiversity, there is much debate over how to predict the species loss that will occur following habitat destruction. In this chapter, I develop a framework to predict the effects of habitat destruction, which occurs through the removal of habitat fragments, or patches, in fragmented landscapes, on local patch species richness by integrating metacommunity theory with the equilibrium theory of island biogeography (ETIB). Metacommunity size is defined as the number of local communities, or patches, that constitute a metacommunity, and habitat destruction is conceptually incorporated into the model by considering the effect of decreasing metacommunity size on patch species richness. Metacommunity size is incorporated into the ETIB through decreasing patch extinction rates or increasing patch immigration rates with increasing metacommunity size, which allows the species richness in small and large patches, and the scaling of species richness between the two patch sizes, to be compared between different sized metacommunities. The species richness in small and large patches, as well as the scaling of species richness between the two patch sizes, depends on whether immigration rates or extinction rates are more affected by metacommunity size. Immigration effects result in species turnover decreasing with metacommunity size, while extinction effects cause species turnover to increase with increasing metacommunity size. The results of this model provide interesting implications for the effect of habitat destruction, or a reduction in metacommunity size, on species richness in both small and large patches within a metacommunity.

Introduction

Habitat destruction is a major cause of both local and global species extinctions (Millennium Ecosystem Assessment 2005) because it can result in both a reduction of total habitat area and habitat fragmentation (Fahrig 2003). Despite habitat destruction being the largest anthropogenic threat to biodiversity (Sala et al. 2000), there is continuing debate over how to predict the amount of species loss that will occur following habitat destruction (e.g. Brooks et al. 2002, He and Hubbell 2011, Hanski et al. 2013, Rybicki and Hanski 2013, Matias et al. 2014). Here, I develop a framework to predict the effects of habitat destruction, which occurs through the removal of habitat fragments, or patches, in fragmented landscapes, on local patch species richness by integrating metacommunity theory with the equilibrium theory of island biogeography.

One traditional approach to measuring the effects of habitat destruction on species richness is using the backward Species Area Relationship (SAR). The SAR is among the most well known phenomena in ecology, and describes the general relationship between habitat area and the number of species sampled (MacArthur & Wilson 1967, Schoener 1976, Connor and McCoy 1979, Rosenzweig 1995, Lomolino 2000, Drakare et al. 2006). The most common model formulation of the positive relationship between area and species richness is the power law formulation, $S = CA^z$, where S and A are species richness and area, respectively, and C and z are curve-fitting parameters (Arrhenius 1921, He and Legendre 1996). This equation can be log-transformed to take on the linear form, $\log S = \log C + z \log A$, where z describes the rate of accumulation of species richness with increasing area. In addition to being used to describe regional richness and the scaling of species richness with area, the backwards SAR has been used to incorporate

the effects of habitat destruction on species richness across spatial scales (Diamond 1972, Pimm and Askins 1995, Rosenzweig 1995, Brooks et al. 1999, Ney-Nifle and Mangel 2000). Current research has focused on the efficacy of predictions made using the backwards SAR, and whether the SAR has the potential to over estimate (He and Hubbell 2011, He and Hubbell 2013) or under underestimate (Hanski et al. 2013, Rybicki and Hanski 2013, Halley et al. 2013, Matias et al. 2014) the amount of species loss following habitat destruction.

Despite the popularity of using SARs to model habitat destruction, SARs do not explicitly account for fragmented patches across a landscape, which is the reality for many natural ecosystems that are at risk of further habitat destruction, such as forest and prairie fragments and wetlands. Metacommunity theory explicitly considers a patchy landscape, as well as the interactions between local patches and the regional landscape context in which a patch resides (Leibold et al. 2004, Holyoak et al. 2005). Thus metacommunity theory provides a useful framework for understanding species richness across spatial scales. A metacommunity is a set of local communities, or patches, linked by the dispersal of potentially interacting species (Wilson 1992, Leibold et al. 1994). Species dispersal affects patch immigration and extinction rates, which influence species richness within and among patches of a metacommunity.

One feature of metacommunities that can be particularly important for species richness, but has been under explored, is the influence of the overall size of a metacommunity on species richness within that metacommunity. Metacommunity size can be defined as the number of local communities, or patches, that constitute a metacommunity (Munguia and Miller 2008, LeCraw et al. 2014). Since anthropogenic

influences are increasingly converting fragments of suitable habitat into non-suitable habitat, the size of a metacommunity embedded within an inhospitable matrix is an increasingly important metric for understanding the processes that influence species richness at local and regional spatial scales.

As metacommunity size increases, more species will be found simply due to extinction/colonization dynamics (MacArthur and Wilson 1967) or passive sampling effects (Connor and McCoy 1979). This relationship between species richness and area follows the general pattern of the SAR. Incorporating metacommunity size into ecological models can provide a richer understanding of the importance of total habitat area for species richness patterns in fragmented landscapes. Conceptually, habitat destruction can be incorporated into metacommunity theory through a reduction in metacommunity size, or the number of patches in a metacommunity.

Since patches within a metacommunity are linked through species' dispersal, immigration and extinction dynamics can play an important role in determining patch species richness within a metacommunity (Munguia and Miller 2008). The influence of species' immigration and extinction rates on the species richness of an area is explicitly considered by the equilibrium theory of island biogeography (ETIB), which is also a mechanism underlying the SAR. Through combining metacommunity theory with the ETIB, patch species richness in metacommunities of different sizes can be described using the SAR. According to the ETIB, the equilibrium number of species on an island, or patch, is determined by its area and isolation, which affect patch extinction and immigration rates. Metacommunity size can be incorporated into the ETIB by altering patch extinction and immigration rates with the number of patches, or size, of a

metacommunity. By comparing the species richness in small and large patches embedded within different sized metacommunities, I theoretically explore how changes in metacommunity size can alter the scaling of species richness across patches of different size.

Model

The equilibrium theory of island biogeography (ETIB) states that the equilibrium number of species (\hat{S}) on an island is a function of the maximum immigration rate (I), maximum extinction rate (E), and the number of species in the mainland pool (P), such that

$$\hat{S} = \frac{IP}{I + E} \quad (1)$$

Two assumptions must be made in order to derive a species area relationship (SAR) using the ETIB (MacArthur and Wilson 1963, 1967). First, population sizes of each species must be proportional to island area, and second, species extinction rates decrease with increasing population sizes. With these assumptions, large islands will have relatively larger population sizes and lower extinction rates than small islands, and thus have more species (Ryberg and Chase 2007) (Figure 1.1B). In log-transformed SARs the slope of the line, z , represents the increase in equilibrial species number from small (\hat{S}_S) to large (\hat{S}_L) islands divided by change in area from small (A_S) to large (A_L) islands (Figure 1.1F):

$$z = \frac{\log \hat{S}_L - \log \hat{S}_S}{\log A_L - \log A_S} \quad (2)$$

To make the transition from predicting the slope of the SAR between two different size islands, to the slope of two patches in a metacommunity, a number of assumptions must be made. In this model, a given metacommunity is made up of an

equal number of small and large patches. This allows z to be calculated as the difference in the expected number of species in a small versus a large patch within a metacommunity. Metacommunity patch sizes of small and large become analogous to small (A_S) and large (A_L) islands. Likewise, the mainland species pool (P) becomes the regional species pool of the metacommunity. Metacommunity size is manipulated by changing the number of patches a metacommunity contains. A representative “large” metacommunity contains more habitat patches than a comparable “small” metacommunity (Figure 1.1C). Conceptually, when metacommunity size increases, the average area of patches in a metacommunity, the average patch isolation, and the habitat type remains constant. Thus, the primary effect of increasing metacommunity size is increasing the total amount of habitat area in the metacommunity.

I modified the ETIB in two ways to investigate how SARs vary with changes in metacommunity size. First, species’ immigration rates into habitat patches of a metacommunity can increase with increasing metacommunity size through the target effect (Gilpin and Diamond 1976). With the target effect, dispersers are more likely to be intercepted by suitable habitat within a large metacommunity than a small one (Lomolino 1990). I assume that the increase in immigration rate with metacommunity size is the same across all species in the regional pool. If immigration rate increases with metacommunity size (I_{Msize}), the scaling of species richness with area, or the slope, z , of the SAR becomes:

$$z = \frac{\log(\frac{I_{Msize} + E_S}{I_{Msize} + E_L})}{\log(\frac{A_L}{A_S})} \quad (3)$$

where E_S and E_L are extinction rates for small and large patches within a metacommunity, and A_S and A_L are the areas of small and large patches, respectively (Figure 1.1D). In addition to calculating z , the number of species found in a single small patch located within a metacommunity can be determined through modifying equation (1):

$$S_S = \frac{I_{Msize}P}{I_{Msize} + E_S} \quad (4)$$

This equation can also be used to calculate the number of species found in a large patch within a metacommunity by replacing E_S with E_L .

Changes in metacommunity size may also affect the extinction rate of habitat patches within a metacommunity. When immigration rates are sufficiently high, it can reduce the extinction rate through the rescue effect (Brown and Kodric-Brown 1977). The rescue effect can decrease the extinction rate through demographic and genetic contributions of immigrants which increase the size and fitness of populations, or reduce the apparent extinction rate by decreasing the probability that a given species will be absent during a sampling period (Brown and Kodric-Brown 1977). The rescue effect can be incorporated into the model by adding an additional term, E_{Msize} , to equation (3). E_{Msize} increases linearly with metacommunity size until it is equal to E_L , which allows the net extinction rate ($E_L - E_{Msize}$) to decrease in patches located in large metacommunities up until there is no extinction rate in large patches within a large metacommunity (Figure 1.1E).

$$z = \frac{\log\left(\frac{I + E_S - E_{Msize}}{I + E_L - E_{Msize}}\right)}{\log\left(\frac{A_L}{A_S}\right)} \quad (5)$$

When extinction rates decrease with metacommunity size the number of species found in a single small patch located can be calculated as:

$$S_S = \frac{IP}{I + E_S - E_{Msize}} \quad (6)$$

As with equation (4), this equation can also be used to calculate the number of species found in a large patch within a metacommunity by replacing E_S with E_L .

Results

When immigration increases with metacommunity size through the term I_{Msize} , the slope of the SAR, z , decreases (Figure 1.2). The source of this reduction in z with increasing metacommunity size becomes apparent when comparing the species richness in small versus large patches in representative small and large metacommunities (Figure 1.3A). Z is reduced in large metacommunities due to a larger increase in species richness of small patches relative to large patches when compared to the species richness in a small metacommunity (Figure 1.3A). The relative change in z between small and large metacommunities can be visualized from the slope of the lines connecting small and large patch species richness (Figure 1.3A).

Conversely, when the net extinction rate decreases with metacommunity size through an increase in the term E_{Msize} , z values increase (Figure 1.2). Z increases in large metacommunities because there is a larger increase in species richness of large patches relative to small ones when compared to the species richness of patches located in small metacommunities (Figure 1.3B). These results are constant for any parameter value combination where $A_S < A_L$, $E_L < E_S$, and $E_{Msize} \leq E_L$ which are built into the assumptions of the model.

Discussion

The effect of metacommunity size, and thus habitat destruction, on species richness depends on whether species immigration rates or extinction rates are more affected by metacommunity size. When immigration rates increase with metacommunity size, z decreases with metacommunity size (Figure 1.2). This is because the higher immigration rates in large metacommunities cause patches to be more similar in species composition, and thus have lower turnover in species between small and large patches when compared to small metacommunities. When extinction rates decrease with metacommunity size, z increases with metacommunity size (Figure 1.2), and there is higher turnover in species composition between small and large patches within a large metacommunity than within a small metacommunity. If metacommunity size equally affects immigration and extinction rates, then there would be no change in z or species richness of small and large patches in metacommunities of different sizes.

The changes z values in this model are a result of differential effects of metacommunity size on small versus large patch species richness. When immigration rates increase with metacommunity size, species richness increases in both small and large patches, but the relative increase is greater in small patches, reducing the scaling of species richness with area (Figure 1.3A). Decreasing extinction rates with metacommunity size has the opposite effect on species richness, in that it increases more in large patches relative to small ones, increasing the scaling of species richness with area (Figure 1.3B). The differential effects of immigration and extinction rates on species richness in small and large patches, or spatial scales, has interesting implications for predicting species loss following habitat destruction.

When metacommunity size alters immigration rates, then habitat destruction, represented by a reduction in metacommunity size, will result in more species extinctions than predicted by the pre-destruction (large) metacommunity (Figure 1.3A). With immigration effects, species loss following habitat destruction via a reduction in metacommunity size will be greater in small patches relative to large patches. (Figure 1.3A). Conversely, if metacommunity size alters extinction rates, then habitat destruction will have little effect on the species richness of small patches within a metacommunity, but result in a more severe loss in species richness in large patches (Figure 1.3B). This model suggests that the effect of habitat destruction on metacommunity species richness will depend on whether species' immigration or extinction rates are more sensitive to changes in metacommunity size. However, if immigration and extinction rates do not respond to changes in metacommunity size, or respond in a complementary manner, then there would be no effect of a reduction in metacommunity size through habitat destruction on small or large patch species richness.

The habitat destruction implications of this model complement recent habitat destruction and species loss literature. In metacommunities with immigration effects, species richness after habitat destruction is less than predicted from the initial (large metacommunity) conditions in both small and large patches (Figure 1.3A). Species richness is also less than predicted in large patches within metacommunities with extinction effects (Figure 1.3B). These results are congruent with recent studies that have asserted the SAR underestimates species loss following habitat destruction (Hanski et al. 2013, Rybicki and Hanski 2013, Halley et al. 2014, Matias et al. 2014). The SAR calculated in this model is a curve produced from two 'isolates' (Preston 1962), or a type

IV curve (Scheiner 2003) calculated from different sized islands. An isolates SAR is different from the SAR of a continuous landscape, which is typically considered when using the backwards SAR to predict species loss following habitat destruction.

Modifications to continuous SARs are the basis of many recent habitat destruction models (e.g. He and Hubbell 2011, He and Hubbell 2013, Matias et al. 2014). However, an isolates SAR is an appropriate method for estimating species loss in fragmented landscapes (Halley et al. 2014), which is the purpose of this model.

There are a number of assumptions built into this model, and the implications of relaxing some of these assumptions can be considered. The ETIB assumes that species do not interact, species' population sizes are constant and proportional to patch area, and extinction rates are inversely proportional to population size (MacArthur and Wilson 1963, 1967). In addition, other assumptions were made in the model with respect to metacommunity structure including that metacommunities have an equal number of small and large sized patches, and average patch area and isolation are constant in metacommunities of different size.

An equal number of small and large patches in metacommunities of different sizes creates a direct relationship between metacommunity size and total habitat area. If this assumption was relaxed, a different modeling technique would be needed (i.e. simulation modeling). However, the patch size of small and large patches can be allowed to vary between metacommunities. If patch size varies, there is still an effect of metacommunity size, but the strength of that effect depends on the magnitude of the habitat size differences between small and large patches. If there is a small difference in the size of large and small patches, $\log(A_L/A_S) < 1$, then z values will be higher overall. Conversely,

if there is a large difference between the size of large and small patches, $\log(A_L/A_S) > 1$, z values will be lower overall. In both cases, the relationship between z and metacommunity size does not change, only the magnitude of z .

Metacommunities can vary in their isolation of local patches, and these differences in patch isolation might influence the mechanisms by which metacommunity size affects species richness in local patches. In isolated metacommunities, extinction effects are likely to be stronger than immigration effects because even though isolation limits dispersal between patches, large metacommunities can still maintain larger population sizes of species since they contain a larger amount of habitat area for more individuals, thus reducing the extinction rate of species at the level of the entire metacommunity. In order to make biologically useful predictions about the degree of isolation necessary for immigration or extinction effects to become more influential, information is needed about the dispersal abilities of the organisms of interest, as dispersal abilities are known to play an important role in structuring both aquatic (De Bie et al. 2012) and terrestrial (Driscoll 2008) metacommunities. Habitat matrix can also influence species dispersal rates (Ricketts 2001), and altering the severity of the habitat matrix through immigration rates is another way to indirectly incorporate isolation into the model.

Many habitat destruction prediction approaches are based in continuous landscapes and at continental scales. This model operates at a regional, metacommunity, scale where individual communities share a common regional pool (P). The metacommunity scale is appropriate for many management and conservation applications because it is the level at which data are collected and management plans are

implemented. In order to test the applicability of this model to natural systems, replicate metacommunities with similar sized regional pools but different number of patches are needed. Data from replicate natural metacommunities are rare if they exist, and only two experiments have directly manipulated metacommunity size (Munguia and Miller 2008, LeCraw et al. 2014). Both experiments found that metacommunity size influenced species richness and composition, suggesting that metacommunity size may be an important factor in influencing the scaling of species richness with area in natural systems. Although the effect of metacommunity size in these studies depends on dispersal ability (Munguia and Miller 2008) or species functional group (LeCraw et al. 2014).

In this model, all species and individuals are equal. However, dispersal ability and life history characteristics might influence whether organisms' immigration or extinction rates are more affected by metacommunity size. Widespread passive dispersers, such as zooplankton and wind dispersed plants, may be more likely to have immigration rates affected by changes in metacommunity size since these organisms depend on passively encountering suitable habitat. Conversely, active dispersers may be more likely to be affected by extinction effects since they might preferentially pick some habitats over another within a metacommunity (e.g. Binckley and Resetarits 2005, 2007), ultimately lowering the extinction rate in that particular patch through the rescue effect. Thus, we expect that dispersal mode can lead to differences in species richness scaling. In a meta-analysis across ecosystems and environments Soininen et al. (2007) found that passively dispersing organisms have lower turnover in species richness between local and regional spatial scales than active dispersers.

This model combines the equilibrium theory of island biogeography and metacommunity theory to make predictions on the effect of metacommunity size on species richness scaling. I found that the effect of metacommunity size on species richness depends on whether species' immigration or extinction rates are more affected by changes in metacommunity size. The results of this model provide interesting implications for the effect of habitat destruction, or a reduction in metacommunity size, on species richness in both small and large patches within a metacommunity.

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Figure 1.1: Conceptual figure of model. A_S and A_L represent the area of small islands/patches and large islands/patches, respectively. Likewise, S_S and S_L is the species richness on small and large islands/patches, and E_S and E_L are the respective extinction rates. I is the immigration rate into an island or patch, and P is the regional species pool. Z is the slope of the Species Area Relationship (SAR). (A and B) Conceptual diagram using the equilibrium theory of island biogeography to understand the effect of island area on species richness. (C) Conceptual diagram of the metacommunity size framework used in this model. (D) Effect of immigration rate increasing with metacommunity size (I_{Msize}) incorporated into the equilibrium theory of island biogeography. (E) Effect of net extinction rate (e.g. $E_L - E_{Msize}$) being reduced with increasing metacommunity size through an increase in E_{Msize} . (F) Using the number of species found in a small island or patch versus a large island or patch to calculate the slope (z) of the SAR.

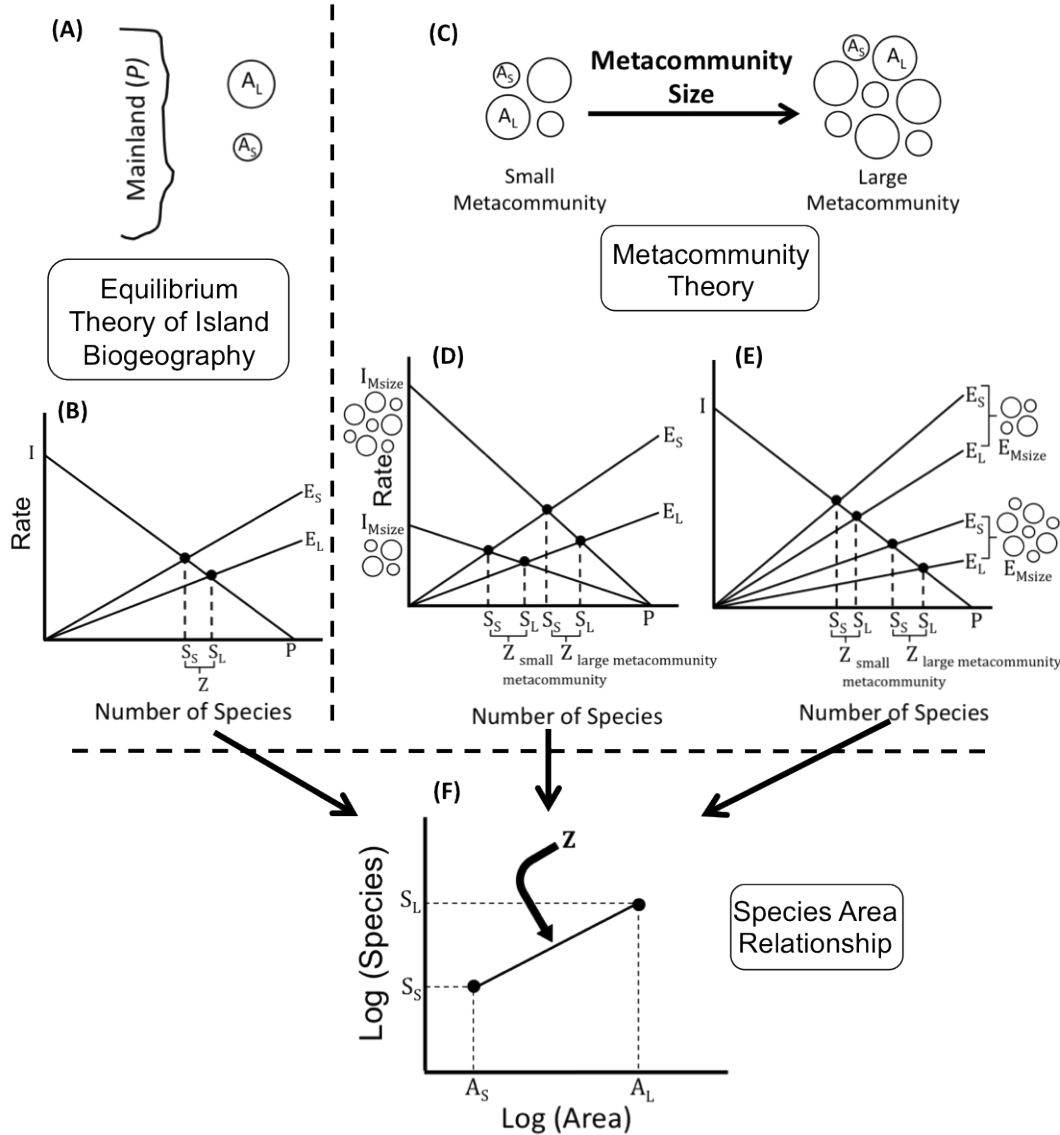


Figure 1.2: Effects of increasing immigration rate (*white circles*) or decreasing extinction rate (*black circles*) with metacommunity size on z values. Immigration results are shown for increasing values of I_{Msize} and $A_S = 10$, $A_L = 100$, $E_L = 0.13$, and $E_S = 0.25$. Extinction results are shown for increasing values of E_{Msize} (which results in an overall decrease in extinction rate) and $A_S = 10$, $A_L = 100$, $E_L = 0.13$, $E_S = 0.25$, and $I = 0.12$.

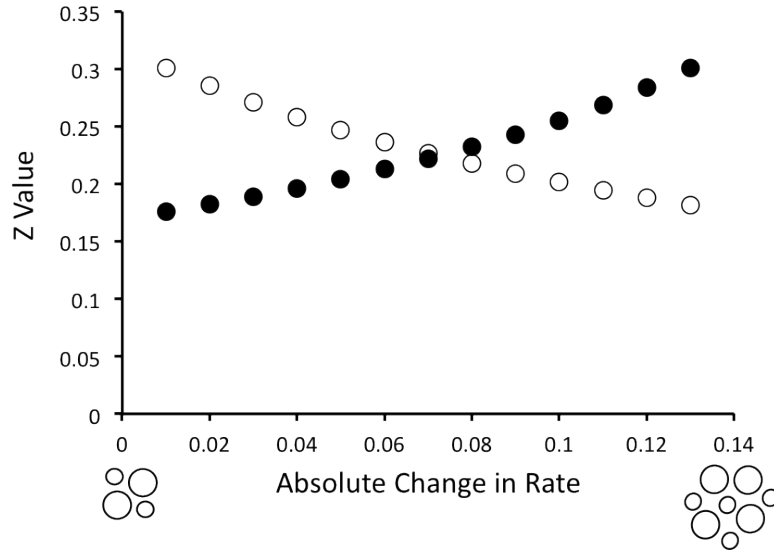
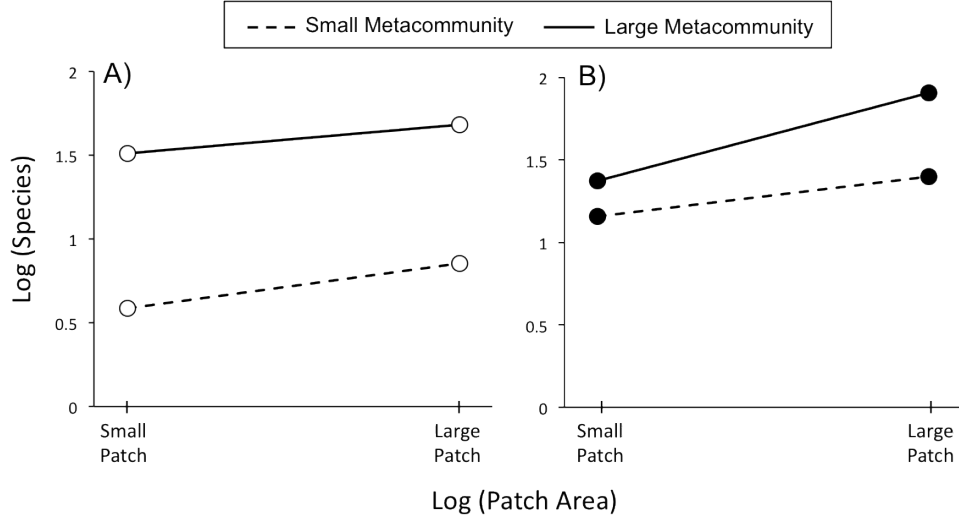


Figure 1.3: The effect of changes in metacommunity size on species richness in small and large patches. The relative change in z between small and large metacommunities can be visualized from the slope of the lines connecting small and large patch species richness. A) The effect of increasing immigration rate with metacommunity size on species richness in small ($A_S = 10$) and large ($A_L = 100$) patches. Small metacommunities have a value of $I_{Msize} = 0.01$ and large metacommunities have a value of $I_{Msize} = 0.12$. Results are shown for $E_S = 0.25$, $E_L = 0.13$, and $P = 100$. B) The effect of decreasing net extinction rate with metacommunity size on species richness in small and large patches. Small metacommunities have a value of $E_{Msize} = 0.01$, and a higher net extinction rate, and large metacommunities have a value of $E_{Msize} = 0.12$, and a lower net extinction rate. Results are shown for $I = 0.04$, and the parameter values of A_S , A_L , E_S , E_L , and P the same as in the immigration scenario (A).



Chapter 2

**The effect of metacommunity size on zooplankton species
richness at different spatial scales in Missouri ponds**

Abstract

Species richness in individual communities and across a landscape is a result of processes and dynamics occurring at both local and regional spatial scales.

Metacommunity theory can be used to understand patterns of species richness in local communities and at the regional, landscape scale. A metacommunity is a group of local communities, or patches, connected by dispersal, and the number of discrete local patches defines the size of a metacommunity. I examined the influence of metacommunity size on species richness at local and regional spatial scales by conducting a field survey of zooplankton species in replicate pond metacommunities. Over two years, 62 ponds from 11 different replicate metacommunities, which varied in metacommunity size (i.e. the number of ponds they contained), were sampled. I found that metacommunity size has scale-dependent effects on zooplankton species richness. As the number of ponds in a metacommunity increase, the species richness of local ponds increases, but there is no change in richness at the regional spatial scale due to decreases in the turnover of species among communities. Additionally, there is an increase in species evenness at the metacommunity level in metacommunity size increases. The results of this study are similar to those of other studies examining the effects of metacommunity size on species richness patterns, and they provide one of the first examples of species richness patterns changing with metacommunity size in a non-experimental system.

Introduction

Species richness in individual communities and across a landscape results from the interplay between processes and dynamics occurring at both local and regional spatial scales (Ricklefs 2004, Leibold et al. 2004, Harrison and Cornell 2008). Metacommunity theory explicitly considers the interaction between local and regional scales (Leibold et al. 2004, Holyoak et al. 2005), providing a useful framework for understanding the partitioning of species richness across spatial scales. A metacommunity is defined as a group of local communities, or patches, connected by dispersal (Wilson 1992, Leibold et al. 2004), and the number of discrete local patches defines the size of a metacommunity. Metacommunity size may be important for patterns of species richness at local and regional spatial scales, but its effects on metacommunity richness are just beginning to be explored (Munguia and Miller 2008, LeCraw et al. 2014).

Metacommunity size might influence species richness at a regional scale by simply having more area to support more species (Connor and McCoy 1979), influence species richness in a local patch by altering dispersal rates among patches within the metacommunity (Mouquet and Loreau 2003), and influence the relationship between local patch size and species richness (Chapter 1). Our understanding of how metacommunity size affects patterns of species richness has come from experimental manipulations (Miller and Munguia 2008, LeCraw et al. 2014), but no researchers have investigated these patterns in naturally occurring metacommunities. These experiments found that metacommunity size influences species richness and composition, suggesting that metacommunity size may be an important factor influencing species richness in more natural systems.

Predictions for how metacommunity size might affect species richness at different spatial scales can be visualized using a species accumulation curve (SAC) (Figure 2.1), in which the number of species increases with the amount of area sampled in a non-linear decelerating fashion (Chase and Knight 2013). These metacommunity size predictions can also be illustrated through plotting how local and rarified regional species richness, as well as species turnover among communities, changes with an increasing number of patches in a metacommunity (Figure 2.2). As metacommunity size increases more species will be found, even in the absence of any habitat heterogeneity, simply due to extinction/colonization dynamics (MacArthur & Wilson 1967) or passive sampling effects (Connor & McCoy 1979). This scenario presents a null expectation where changing the size of a metacommunity is not expected to change the shape of the SAC. As a result, the number of species that occur locally and regionally, as well as other aspects of diversity (e.g., compositional turnover among communities) should not vary between small and large metacommunities (Figures 2.1 and 2.2, solid line).

Deviations from this null expectation of no metacommunity size effect can occur if the basic properties of the metacommunity, such as the size of the species pool and rates of colonization/extinction, vary with metacommunity size. For example, larger metacommunities contain more habitat area, more total individuals, and thus larger species pools (Wright 1983, Srivastava and Lawton 1998). Dispersal rates into local communities from this larger species pool might also increase with metacommunity size and thus increase species richness at local scales (e.g. MacArthur and Wilson 1967, Ricklefs 1987, Mouquet and Loreau 2003, Ricklefs 2004, Harrison and Cornell 2008). If metacommunity size increases local richness through increased dispersal, but has no

influence on rarified regional richness, the shape of the SAC should be shallower in a large metacommunity. This implies there is a lower turnover of species among localities in a large (Figures 2.1 and 2.2, dotted line) relative to a small metacommunity (Figures 2.1 and 2.2, solid line).

Alternatively, metacommunity size might increase rarified regional species richness (Figures 2.1 and 2.2, dashed line). If dispersal rates of organisms increase in larger metacommunities, then metacommunity extinctions could be reduced through rescue effects (Brown and Kodric-Brown 1977). Additionally, the metapopulation sizes of species would increase in larger metacommunities, which might allow some species to persist that might not be able to persist in smaller metacommunities. Here, no change is expected in the local richness between small and large metacommunities, but an increase in rarified regional species richness and turnover in large metacommunities when compared to small ones (Figures 2.1 and 2.2, dashed line).

It is also possible that both local and regional species richness increase in large metacommunities through a combination of increased dispersal rates into local communities (e.g. MacArthur and Wilson 1967, Ricklefs 1987, 2004, Mouquet and Loreau 2003, Cornell and Harrison 2008) and a reduction of extinctions at the level of a metacommunity via rescue effects (Brown and Kodric-Brown 1977). If metacommunity size increases both local and regional species richness then the SAC will increase at both spatial scales, however there will be little or no change in the turnover of species when compared to a small metacommunity (Figures 2.1 and 2.2, dot-dashed line).

Freshwater ponds are an excellent system for studying metacommunity dynamics because of the discrete nature of aquatic habitats embedded within an uninhabitable

terrestrial matrix (Cottenie et al. 2003). Within these ponds, zooplankton, including crustaceans (copepods and cladocerans) and rotifers, represent a diverse group of species and are integral to aquatic ecosystems (Pennak 1989, Shurin et al. 2000). Zooplankton disperse readily between ponds via animals and wind in a mostly random fashion (Maguire 1959, 1963, Jenkins and Buikema 1998, Allen 2007, Frisch et al. 2012), making them ideal organisms for studying metacommunity dynamics. I sampled replicate zooplankton metacommunities containing varying numbers of ponds (patches) to quantify the effects of metacommunity size on local and rarified regional species richness as well as species turnover in a naturalized system.

Methods

A large-scale survey of fishless ponds in Missouri was conducted during the summers of 2009 and 2010 to investigate the importance of metacommunity size on species richness at different spatial scales. In east-central Missouri, where this study takes place, few natural ponds exist because of the karst geology (Unklesbay and Vineyard 1992). However, a large number of ponds have been constructed especially for wildlife and conservation purposes (Shelton 2005). These ponds are often aggregated within public lands providing replicate pond metacommunities for study. Over two years, a total of 62 ponds from 11 different metacommunities were sampled. For this study, metacommunity size is defined as the number of fishless ponds in a metacommunity (Figure 2.3). For a fishless pond to be included in a metacommunity it must be within 1500m of another pond. Pond isolation was measured as the average distance to nearest pond within a metacommunity using ArcGIS (v. 9.3, ESRI, Redlands, California). For this study, the number of ponds in a metacommunity is not correlated

with pond isolation ($P > 0.05$, Table 2.1). Additionally, ponds within a metacommunity were sampled in a manner to ensure that both the distance between sampled ponds and the average area of sampled ponds did not vary with metacommunity size ($P > 0.05$, Table 2.1).

Approximately two liters of water was collected from ten separate locations around each pond (20L total) and filtered through a 80 μ m zooplankton net. This sampling method is comparable to other studies in similar pond ecosystems (Leibold 1999, Steiner 2004). Samples were concentrated to 50 mL and preserved with Lugol's iodine for later identification under a compound microscope using taxonomic keys and a library of preserved taxa with known identifications from the sampling sites (Chase et al. 2010). Due to potential differences in proportional sampling effort in ponds of different sizes, I estimated species richness using Chao's (1984) non-parametric method for extrapolating the total number of species in a pond using abundance data. Chao values for each pond were calculated using the *chao1* function in the fossil package in R (Vavrek 2012). Since the results of this study are the same using Chao estimates of species richness or actual measured richness (Table 2.1), I present results for the actual measured species richness.

Environmental data for each pond was also collected at the time of sampling. Additional water samples were collected for later analysis of total nitrogen and total phosphorus using a Hach DR 2800 Spectrophotometer and following the standard procedures of the Hach methods (HACH Company, Loveland, Colorado, USA). At each pond, data were collected on pond area, canopy cover, and surrounding habitat type which was classified as oak hickory forest, oak hickory and open, oak hickory and other

forest, prairie or wetland, or open habitat. A Principle Components Analysis was conducted to minimize correlations between variables and to determine 3 axes that explained 81.7% of the variation of the environmental variables (Table 2.2). In order to ensure environmental variables were not a better predictor of species richness than metacommunity size, a GLM was used to test for the effects of the environmental PCA axes on local pond species richness. None of the environmental axes were significant predictors of pond species richness ($p > 0.10$), so pond environment was not considered in future analyses.

Species turnover for each metacommunity was measured from the slope, z , of the Species Area Relationship (SAR). The most common model formulation of the SAR is $S = CA^z$, where S and A are species richness and area, respectively, and C and z are curve-fitting parameters (Arrhenius 1921, He and Legendre 1996). This equation can be log-transformed to take on the linear form, $\log S = \log C + z \log A$, where z describes the rate of accumulation of species, or species turnover, within an area. Large z values represent high species turnover among communities, while low z values represent low species turnover. A z value for each metacommunity was determined using a function created in R (R Core Development Team 2014). For each metacommunity, the order in which ponds were sampled was randomized without replacement, and a species accumulation curve was generated for the number of species found with an increasing number of ponds sampled. This accumulation was log-transformed creating a log-transformed SAR (total number of species sampled versus number of ponds sampled), and the slope of this relationship, z , was calculated using linear regression. This randomization procedure was repeated 9999 times for each metacommunity, and an average z value for each

metacommunity was obtained by averaging the resulting z values from each of the 9999 runs.

Since the slope of the SAR can change due to differences in the number of individuals or shifts in the relative abundances of species (Chase and Knight 2013), another method is needed to disentangle the mechanism causing changes in species turnover. ENS_{PIE} is a metric that can be used to describe changes in species relative abundances, and is a measure of the “Effective Number of Species” in a community (Chase and Knight 2013). ENS_{PIE} is derived from Hurlbert’s PIE and calculated as $1/\sum_{i=1}^S p_i^2$, where S represents the number of species and p_i is the proportion of the community represented by species i (Jost 2006, Dauby and Hardy 2012). Since ENS_{PIE} measures the slope at the base of the SAC, it is not influenced by the extent of sampling, provided species are not aggregated, and can be used to compare the difference in the relative abundances of species among communities (Dauby and Hardy 2012, Chase and Knight 2013). ENS_{PIE} was calculated for individual ponds and for each metacommunity to investigate shifts in the relative abundance, or evenness, of species as both local and regional spatial scales.

If average pond ENS_{PIE} increases with metacommunity size, then the relative abundances of species in ponds are becoming more even, on average, in ponds located within larger metacommunities. Likewise, if ENS_{PIE} decreases, pond relative abundances are becoming less even. Pond evenness can increase through common species becoming less common, or rare species becoming less rare, and a change in average pond evenness can occur with or without a change in average pond species richness. If metacommunity ENS_{PIE} increases with metacommunity size, it indicates that the relative abundances of

species summed across all five sampled ponds is becoming more even with increased metacommunity size. If metacommunity ENS_{PIE} decreases with metacommunity size, the relative abundance of species in a metacommunity is becoming less even.

Metacommunity ENS_{PIE} describes species evenness across the entire metacommunity, which can change independently of average pond ENS_{PIE} .

The relationship between metacommunity size and average local species richness, rarified regional richness (species richness per 5 ponds), z , number of individuals per pond, average pond ENS_{PIE} , and metacommunity ENS_{PIE} was analyzed using linear regression in R (R Core Development Team 2012).

Results

Measures of species richness and species turnover vary with metacommunity size (Figure 2.4, Table 2.1). Average local species richness increases with the number of ponds in a metacommunity, or metacommunity size (Figure 2.4A). However, rarified regional species richness does not vary with metacommunity size (Figure 2.4B). Z values, which are a measure of species turnover among ponds, decrease as metacommunity size increases (Figure 2.4C). There is no relationship between the number of individuals per pond and metacommunity size or the average pond ENS_{PIE} (Table 2.1). However, metacommunity ENS_{PIE} increases with metacommunity size (Figure 2.5). This increase in ENS_{PIE} appears to be due to a reduction in the abundance of common species in large metacommunities compared to small ones (Figure 2.6).

Discussion

The overall results of this field study show that metacommunity size has scale-dependent effects on zooplankton species richness. As the number of ponds in a

metacommunity increase, the species richness of local ponds increases, but there is no change in richness at the regional spatial scale due to decreases in the turnover of species among communities. These patterns match the theoretical predictions for the effect of increased dispersal rates (up to an intermediate rate) on local and regional species richness as well as species turnover (Mouquet and Loreau 2003, Chase et al. 2005).

The increase in local species richness with metacommunity size (Figure 2.4A) may be due to an increase in dispersal rate of individuals among ponds located in larger metacommunities. Increased dispersal rates have been proposed to increase local species richness in a variety of theoretical and empirical studies (e.g. MacArthur and Wilson 1967, Ricklefs 1987, 2004, Mouquet and Loreau 2003, Cornell and Harrison 2008). Although I did not measure zooplankton dispersal rates, it is a reasonable proposed mechanism for the observed change in species richness, especially because landscape factors (e.g. habitat area and isolation) are known to be an important factor in determining local species richness in aquatic systems (Beisner et al. 2006, Thiere et al. 2009, De Bie et al. 2012), and differences in environmental conditions among ponds and between metacommunities was minimized and found not to be an important factor in determining local richness.

I found no affect of metacommunity size on rarified regional richness (Figure 2.4B). This means that increasing metacommunity size does not alter mechanisms that would allow more species to persist at the metacommunity level, such as decreasing the rates of species extirpations as a result of larger population sizes. This pattern of increased local richness with no associated change in regional richness has been theoretically proposed as a response to increasing dispersal rates (Mouquet and Loreau

2003, Chase et al. 2005). Although empirical examples of this pattern are limited, in a study of natural rock-pool metacommunities, Simonis and Ellis (2014) found no change in the regional diversity of invertebrates with increasing dispersal rates from Gulls.

Since rarified regional richness does not change with metacommunity size, but local species richness increases, there is a decrease in species turnover, or z values, with metacommunity size (Figure 2.4C). Increasing metacommunity size has a homogenizing effect of zooplankton communities causing the zooplankton species composition of ponds located in large metacommunities to be more similar to one another than the species composition of ponds located within a small metacommunity. A decrease in species turnover has been proposed to occur with increasing dispersal rates (Mouquet and Loreau 2003, Chase et al. 2005), and numerous studies in natural and experimentally manipulated aquatic systems have found a decrease in species turnover with increased dispersal or connectivity (e.g. Cadotte 2006, Van De Meutter et al. 2007, Vanschoenwinkel et al. 2007, Simonis and Ellis 2014).

At the local level, the increase in species richness with increasing metacommunity size does not appear to result from changes in the number of zooplankton individuals per pond, or changes in species evenness as measured by ENS_{PIE} . However, there is a lot of variation in the number of individuals and ENS_{PIE} among ponds within a metacommunity (Table 2.3). Additionally, there is a small sample size of five ponds per metacommunity, which limits the power for detecting a difference in these metrics between metacommunities.

There is also no change in the number of individuals at the level of rarified regional richness in a metacommunity. However, there is an increase in species evenness

at the metacommunity level as measured by ENS_{PIE} in larger metacommunities.

Theoretical research has shown that factors that increase species evenness will increase species richness at a local scale, decrease species turnover, and have no effect on the regional richness of a simulated community (Chase and Knight 2013). In this study system metacommunity evenness appears to be increased in large metacommunities through a reduction in abundance of the most common species (Figure 2.6). The most abundant species in 9 out of 11 metacommunities is one of two copepod species from the family *Cyclopidae*, *Microcyclops rubellus* or *Mesocyclops edax*. This change in evenness at the metacommunity scale could be a result of increasing metacommunity size altering the outcomes of competition-colonization trade offs (Calcagno et al. 2006) or altering metacommunity trophic dynamics (LeCraw et al. 2014).

The results of this study are similar to those of the two other studies that examine the effects of metacommunity size on species richness patterns (Miller and Munguia 2008, LeCraw et al. 2014). In marine pen shell communities, Munguia and Miller (2008) found higher local community species richness in large metacommunities compared to small ones, but no effect of metacommunity size on regional richness. The experimental student of LeCraw et al. (2014) found higher species evenness in large compared to smaller metacommunities of tropical bromeliads. This research provides one of the first examples of species richness patterns changing with metacommunity size in a non-experimental system.

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Table 2.1: Results from linear regressions with number of ponds in a metacommunity (i.e. metacommunity size) as an explanatory variable and different metacommunity response variables.

Metacommunity response variable	F ratio	Adjusted R^2	P value
Average distance between all ponds	$F_{1,9} = 1.509$	0.0484	0.2505
Average area of sampled ponds	$F_{1,9} = 0.555$	-0.0465	0.4751
Average distance between sampled ponds	$F_{1,9} = 0.618$	-0.0397	0.4519
Average chao estimate of species richness	$F_{1,9} = 7.087$	0.3784	0.0260
Average local species richness	$F_{1,9} = 7.940$	0.4097	0.0201
Rarified regional species richness	$F_{1,9} = 0.407$	-0.0631	0.5396
Average Z value	$F_{1,9} = 17.120$	0.6171	0.0025
Number of individuals per pond	$F_{1,9} = 0.773$	-0.0233	0.4022
Average Pond ENS_{PIE}	$F_{1,9} = 1.694$	0.0649	0.2253
Metacommunity ENS_{PIE}	$F_{1,9} = 4.979$	0.2847	0.0526

Table 2.2: Loadings of environmental variables on the first three axes extracted by PCA, and the proportion of variance accounted for by each axis, for 62 ponds in Missouri.

Variable	PC axes		
	1	2	3
Matrix	-0.106	0.413	0.708
Canopy Cover	-0.330	0.134	-0.628
TN mg/L	-0.704		
TP µg/L	-0.482	-0.599	0.320
N:P	-0.388	0.667	
Proportion of total variance (%)	36.8	23.6	21.3

Table 2.3: The average and standard deviation of the number of individuals per pond and pond ENS_{PIE} for each metacommunity. CA, Conservation Area; SF, State Forest; NR, Nature Reserve.

Metacommunity	Number of ponds	Number of individuals per pond		Pond ENS_{PIE}	
		Average	Standard Deviation	Average	Standard Deviation
Pea Ridge CA	6	343.80	271.60	3.02	1.08
US Forest Service	6	596.00	958.82	3.73	2.28
Busch CA	7	401.60	528.18	2.58	0.69
Little Indian Creek CA	9	524.80	550.50	3.20	1.14
Reifsnider SF	12	160.67	132.59	3.63	0.66
Shaw NR	12	1214.00	2209.41	4.78	2.49
Long Ridge CA	13	210.17	172.18	4.14	1.35
Daniel Boone CA	15	417.43	202.38	2.64	0.90
Danville CA	17	154.40	137.36	3.68	1.16
Meramec CA	20	265.50	78.08	3.46	1.92
Huzzah CA	22	318.33	237.02	4.57	1.79

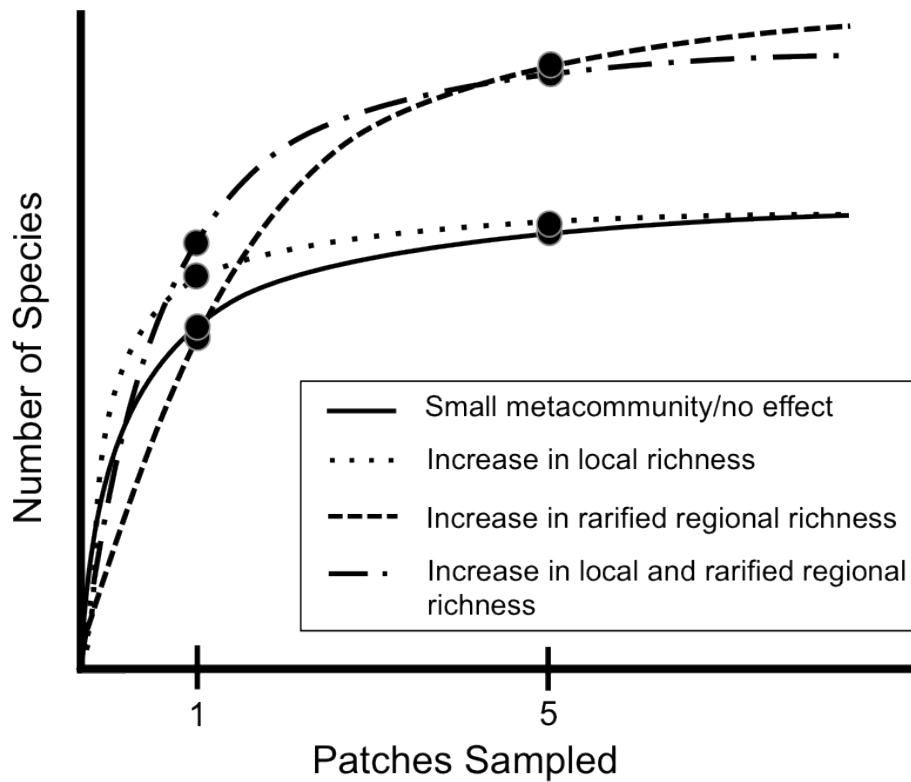


Figure 2.1: Conceptual diagram of the potential effects of increasing metacommunity size on the species accumulation curve (SAC). Points are placed to emphasize how changing the SAC can differentially affect species richness at local scales, or when 1 patch is sampled, and at the rarified regional richness scale, or when 5 patches are sampled. The *solid* line represents the SAC of small metacommunities, and the null expectation of no change in the SAC of large metacommunities. The *dotted* line represents the case when local species richness increases in large metacommunities, decreasing species turnover among communities in large metacommunities relative to small ones. The *dashed* line depicts the scenario when large metacommunities have an increase in rarified regional species richness and thus an increase in species turnover. The *dot-dashed* line represents the scenario when both local and rarified regional species richness increase in large metacommunities and thus there is little or no change in species turnover between small and large metacommunities.

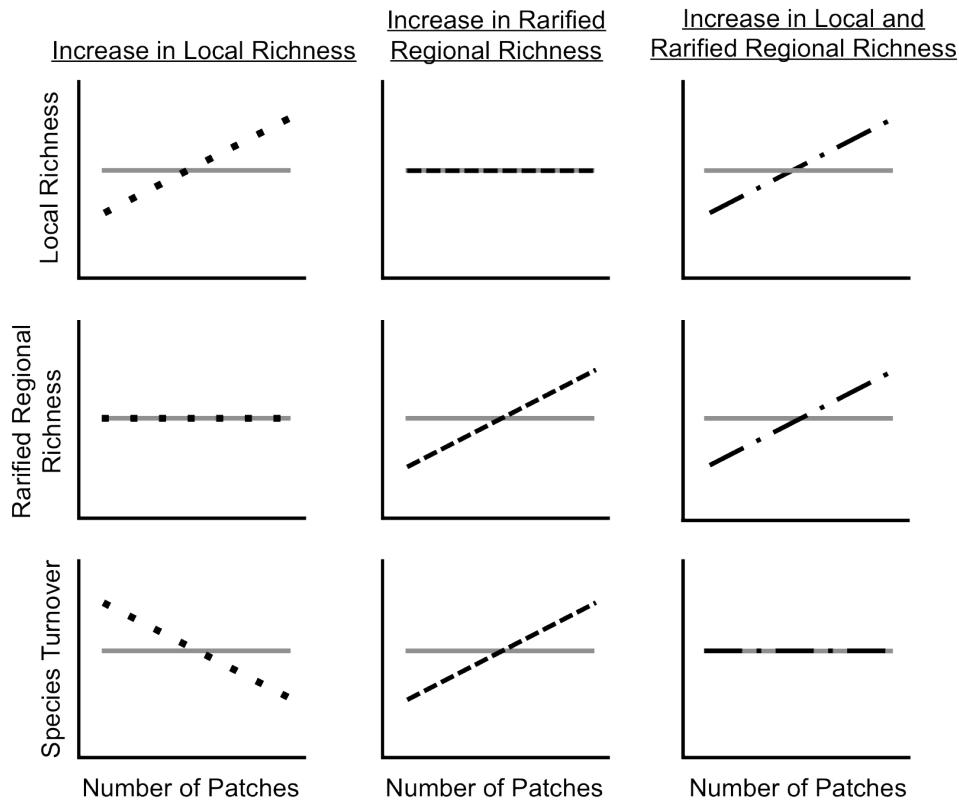


Figure 2.2: Conceptual diagram of the potential effects of increasing metacommunity size on local species richness, rarefied regional species richness, and species turnover. The solid grey line represents the null expectation of no affect of increasing metacommunity size on species richness or turnover, and the black lines represent alternative hypotheses for how metacommunity size might affect species richness and turnover based on the SAC predictions from Figure 1. The left column with the *dotted* lines represents the scenario when local species richness increases with metacommunity size, decreasing species turnover among communities. The middle column with the *dashed* lines depicts the case when metacommunity size increases rarefied regional species richness and decreases species turnover among communities. The right column with the *dot-dashed* lines presents the scenario when both local and rarefied regional richness increase with metacommunity size resulting in little or no change in species turnover among communities.

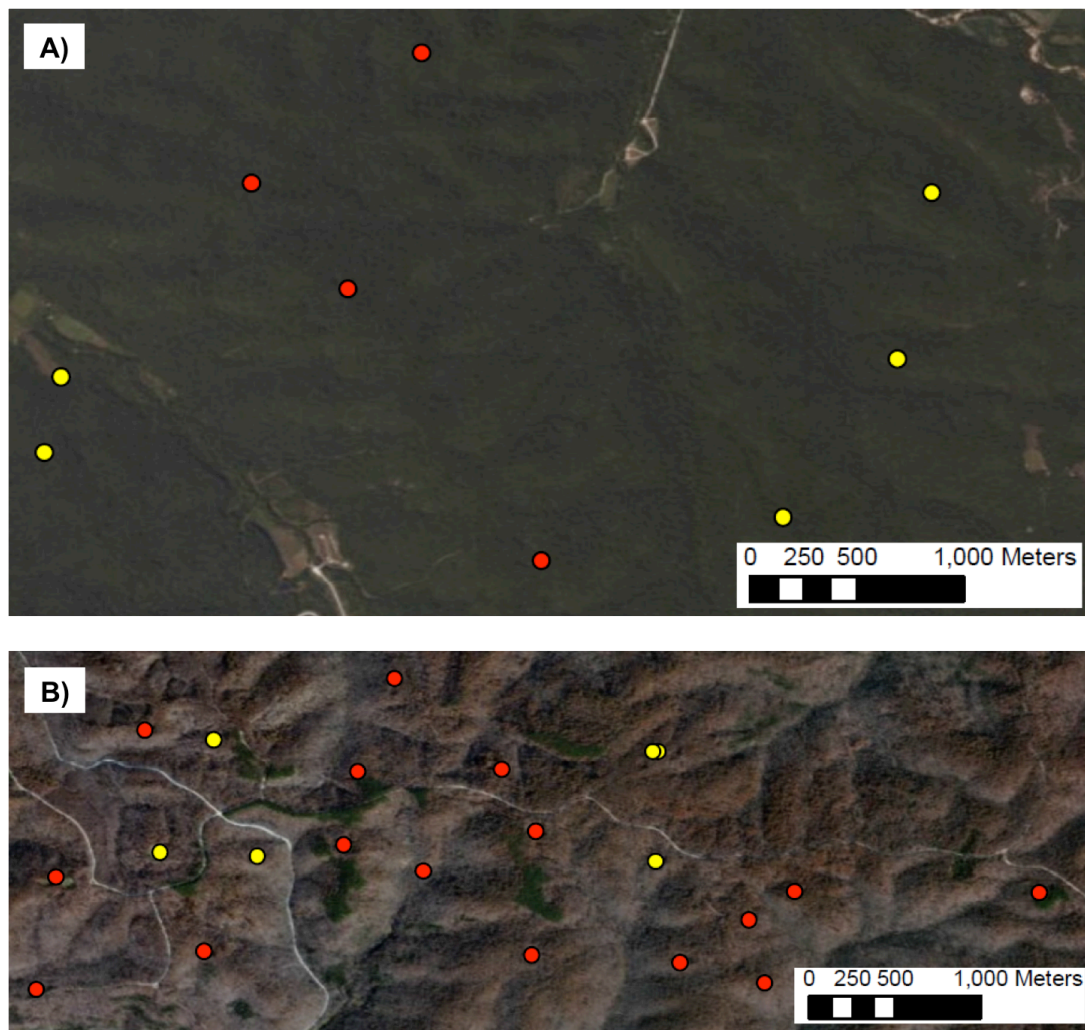


Figure 2.3: Representative small (A) and large (B) pond metacommunities from this study. Each point represents a fishless pond in the metacommunity with sampled ponds denoted in yellow and red circles representing ponds that were within the metacommunity but not sampled. A) Representative small metacommunity with 9 ponds, 5 of which were sampled, and B) a representative large metacommunity with 22 ponds, 6 of which were sampled. Images created using ArcMap 10.2, Source: Esri, DigitalGlobe, GeoEye, i-cubed, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community.

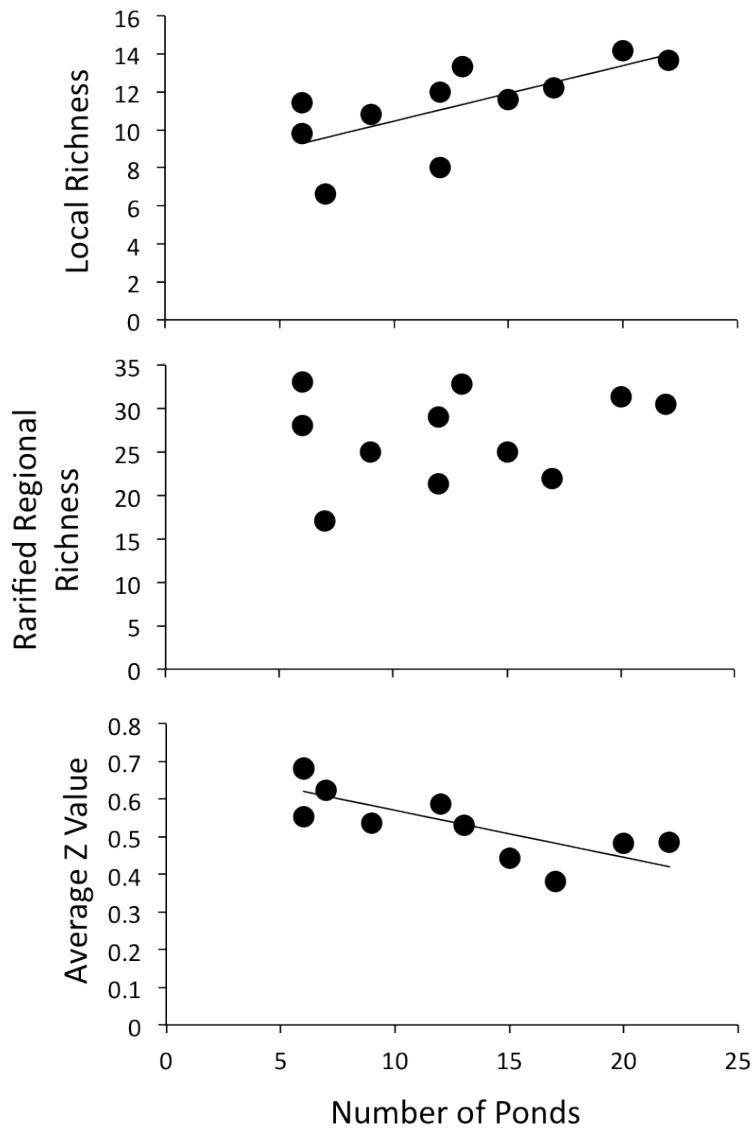


Figure 2.4: A) Increase in the average alpha of a metacommunity with an increase in the number of ponds within a metacommunity ($y = 0.2922x + 7.5378$, $r^2 = 0.4097$, $P = 0.0201$). B) No relationship between the rarified gamma in 5 ponds and the number of ponds in a metacommunity. C) A decrease in the Z-value of a metacommunity with an increase in the number of ponds in a metacommunity ($y = -0.014024x + 0.721422$, $r^2 = 0.6171$, $P = 0.0025$).

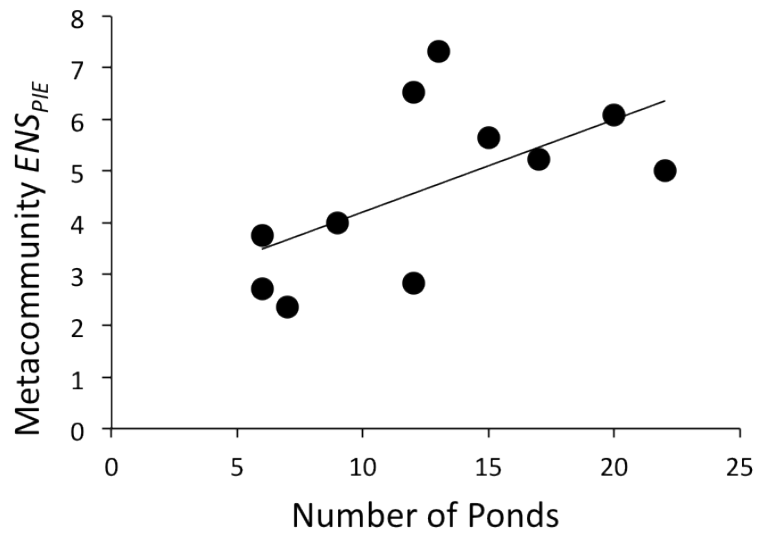


Figure 2.5: Metacommunity ENS_{PIE} increases with increasing metacommunity size ($y = 0.18217x + 2.36301$, $r^2 = 0.2847$, $P = 0.0526$).

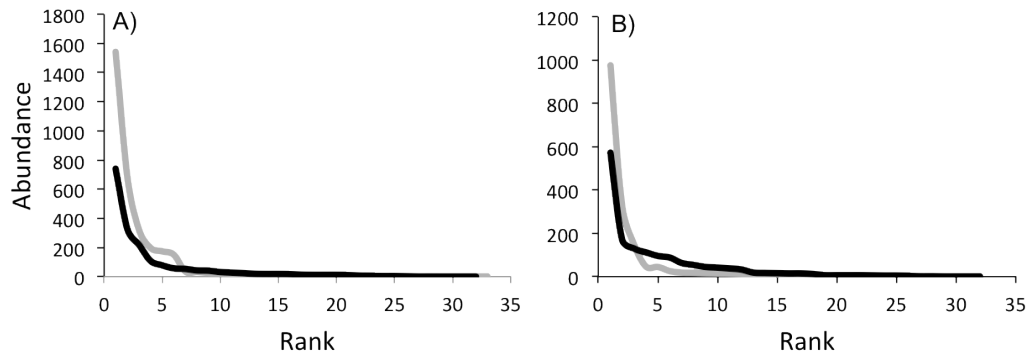


Figure 2.6: Rank abundance distributions (RAD) for the two smallest and largest metacommunities. Small metacommunities are denoted in grey and large metacommunities are in black. A) RAD for a small metacommunity of 6 ponds (US Forest Service) and a large metacommunity of 22 ponds (Huzzah CA). B) RAD of a small metacommunity of 6 ponds (Pea Ridge CA) and a large metacommunity of 20 ponds (Meramec CA).

Chapter 3

Dispersal moderates recovery of wetland plants following drought disturbance

Abstract

Natural disturbances play an important role in altering and maintaining patterns of species richness. However, the frequency and intensity of these disturbances are expected to increase with climate change, likely increasing species loss across ecosystems. Disturbances can have a stochastic or deterministic effect on ecological communities, which result in different changes in species composition and species richness at local and regional scales. I examined the effect of a natural drought disturbance on species richness in aquatic plant communities, and I used a null modeling approach to analyze the relative stochastic or deterministic effect of drought on aquatic plant species. I also investigated whether varying amounts or timing of dispersal influences the recovery of aquatic plant communities following the natural drought disturbance. I found that local species richness decreased in response to drought, and there was a loss of some species from the entire experiment. Species composition was also affected by drought, with aquatic plant communities becoming more similar to one another after the drought. The overall effect of drought on plant species in this experiment was highly selective as 68.75% of species had community occupancies after the drought that were either higher or lower than expected by chance, implying that species were lost as a result of deterministic processes. Increasing species dispersal after the drought disturbance promoted the recovery of species richness. Species richness in all three dispersal treatments recovered to their pre-drought conditions, suggesting that even low amounts of species dispersal can facilitate the recovery of species richness in aquatic plant communities.

Introduction

Natural disturbances play an important role in altering and maintaining patterns of species richness in aquatic and terrestrial ecosystems (e.g. Connell 1978, Sousa 1979, Molino and Sabatier 2001). Changes in the Earth's climate are expected to lead to an increase in the frequency or intensity of natural disturbances such as heat waves, floods, and droughts (Mitchell et al. 2006). These changes in natural disturbance regimes are likely to lead to species loss across ecosystems (Sala et al. 2000), making it crucial to understand how natural disturbances affect species richness, and what processes are essential for the recovery or maintenance of species richness.

Disturbances can affect ecological communities through stochastic processes such as random species extinction (Hubbell 2001), or deterministic processes including species' niche interactions with changing environmental conditions (Chase 2007). A stochastic disturbance results in the random removal of species from local communities and should result in a decrease in local community species richness and a decrease in community similarity (Ostman et al. 2006, Myers and Harms 2011, Chase and Myers 2011, Tonkin and Death 2013). Disturbances can also have a deterministic effect on communities by selectively removing individual species from a regional species pool, resulting in a decrease in local diversity and an increase in community similarity (Chase 2007, Smith et al. 2009, Chase and Myers 2011). The degree to which communities respond to a disturbance stochastically or deterministically can depend on the type and severity of disturbance and the ecological system it occurs in (Cadotte 2007, Jiang and Patel 2008, Lepori and Malmqvist 2009, Myers and Harms 2011, Tonkin and Death 2013).

When communities respond to disturbances deterministically, disturbance acts as an abiotic ecological filter and selectively removes species from a community (Chase 2007, Myers and Harms 2009, Chase and Myers 2011, HilleRisLambers et al. 2012). Only species with traits that are viable under the selective filter of disturbance will remain in a community, although species can also be removed as a result of species interactions (Díaz et al. 1998). Studies have found that ecological communities can be filtered by traits that are suitable to a particular climate (Díaz et al. 1998) or disturbance regime (Haddad et al. 2008). The study of species trait responses to disturbances provides a deeper understanding of community response to disturbance when compared to the traditional approach of only measuring species richness responses (Mouillot et al. 2013).

Following a disturbance, the recovery of species richness depends on the restoration of suitable environmental conditions, species interactions within the disturbed area, and an adequate supply of propagules (Palmer et al. 1997). Furthermore, it is possible that priority effects following disturbance can inhibit the full establishment and recovery of species arriving during the post-disturbance period (Palmer et al. 1997, Louette and De Meester 2007, Louette et al. 2008). Alternatively, species interactions can also be positive and promote the establishment of colonizing species following a disturbance through facilitation (Bertness and Shumway 1993, Young et al. 2001). However, the recovery of species richness is often dependent upon a supply of recruits into the disturbed habitat (Young et al. 2001). In many communities, species richness is limited by the availability of propagules (Robinson and Handel 1993, Young et al. 2001, Flinn

and Vellend 2005, Clark et al. 2007, Myers and Harms 2009) and increased dispersal after a disturbance can increase species richness (Myers and Harms 2009).

In this study I use experimental aquatic plant communities to investigate the effect of a natural drought disturbance on species richness, and the role of dispersal in their recovery. In addition to providing a useful model system in which to evaluate community assembly processes, aquatic plants provide food for waterfowl, nesting and breeding habitats for fish, birds, and other aquatic organisms, erosion control, and wastewater treatment (Whitley et al. 1999). Aquatic plants are also used as indicator species of environmental health (Carbiener et al. 1990, Ceschin et al. 2010). Although they are widely distributed (Santamaría 2002), many species of aquatic plants are dispersal limited when not directly connected via waterways (Capers et al. 2010, Akasaka and Takamura 2012). The reliance of aquatic plants on water pathways for dispersal allowed me to experimentally manipulate dispersal following a natural drought disturbance to investigate the relative importance of dispersal and species interactions for the recovery and maintenance of species richness in these communities.

Methods

During the summer of 2010 an experiment was established at Washington University's Tyson Research Center (Eureka, MO) using 2,200L experimental mesocosms that mimic freshwater ponds to examine the effects of disturbance on aquatic plant communities and influence of dispersal on plant community recovery. A total of 40 mesocosms were established with a 0.18m layer of soil composed of $\frac{1}{2}$ topsoil and $\frac{1}{2}$ compost and filled with water. All mesocosms were then assembled with a diverse array of aquatic plants and algae (Table 3.1) to create replicate aquatic plant communities. At

least one individual, sprig, or aliquot of each plant species was added to each mesocosm, and species were left to become established or go extinct. A diverse assemblage of zooplankton species and two snail species (*Helisoma anceps*, *Physa gyrina*) were also added to the mesocosms to graze on phytoplankton and periphyton and support nutrient cycling within the tanks. Additional aquatic invertebrates and vertebrates naturally colonized the mesocosms over time.

Mesocosms were sampled twice each summer, once early in the season (May/June) and once later in the season (July/August) beginning in 2011, except for 2014 when mesocosms were only sampled once in July. The plant communities in each mesocosm were sampled using a combination of three quantitative quadrats and a survey of additional rare species present within the mesocosm, but not located within the sampling quadrats. Each quadrat was 0.5m² with four 0.5m legs attached to allow it to stand upright in a mesocosm. The water level in the mesocosms varied seasonally, so the depth of water sampled within a quadrat varied by date. Three quadrats were sampled in each mesocosm and species present were assigned a relative percent volume occupied. In some instances, when the water column was full of submerged plants and there were additional emergent plants (e.g. *Sagittaria latifolia* or *Nymphaea odorata*) percent volume could be greater than 100%. For each mesocosm, the percent volume of the three quadrats was averaged to obtain an average percent volume occupied by each species. The relative abundance of species in each mesocosm was based on sampling over 40% of the mesocosm with the three quadrats. Average percent volume was then compiled with the additional rare species present in the mesocosm, which were represented by a percent volume of 1, into a compiled plant community abundance.

Species richness stabilized by the end of the second summer (July 2011 average richness 7.35 ± 1.44 SD) and remained stable into the beginning of the third summer (May 2012 7.2 ± 1.11 SD). However, the summer of 2012 was the most severe summertime drought the Central Great Plains had experienced in 117 years (Hoerling et al. 2014). This drought coincided with the application of an atrazine disturbance treatment to a subset of mesocosms in this study. There was no effect of atrazine on species richness (ANOVA, $P = 0.959$), but there was an effect of drought on all plant communities in the study. Mesocosms were refilled with water and rearranged into new treatments to alleviate any potential legacy effects of the atrazine treatment, and the effect of drought on plant community species richness and composition was investigated.

Plant trait data were collected on extant species in 2014 to examine the role of plant traits in explaining species' differential responses to drought. For each plant species, leaf area and specific leaf area (SLA) were measured. I chose these traits because stressors, including heat and drought, have been shown to select for small leaf area in terrestrial systems (Cornelissen et al. 2003). Specific leaf area, in particular, is associated with fast relative growth rates and high photosynthetic capacity per unit leaf area (Westoby et al. 2002), and may also be an important trait for determining a species' response to drought. Traits were measured on at least 14 individuals, or fragments, of each species. At least one fully formed adult leaf was collected from each of the sampled individuals, and was then blotted dry and immediately weighed and scanned. Leaves were dried at 55°C for 4 days and then weighed to determine leaf dry weight. Individual leaf area was calculated from the leaf scans using Image-J (Rasband 2014). Specific leaf area was calculated as leaf area (cm^2) per unit of dry leaf mass (g). For each species, a

mean trait value was calculated across the measured individuals. Additional plant trait data on morphology, longevity, and fecundity were compiled from Whitley et al. (1999) and Arthaud et al. (2012) (Table 3.1).

Dispersal treatments were established to investigate the relative importance of dispersal limitation on the recovery of plant species richness following drought. Dispersal treatments were designed to test the influence of both the biomass of dispersal and the timing of dispersal on community recovery. A dispersal event consisted of one individual, several sprigs, or an aliquot of each species listed in Table 3.1 (except *Myriophyllum spicatum*). The biomass of a species added to each mesocosm was standardized, and effort was made to add comparable amounts of biomass of different species to mesocosms despite differences in size and growth form. Ten mesocosms were assigned to each of the control and three dispersal treatments for a total of 40 mesocosms. A control group received no additional dispersal following the drought disturbance. A low biomass dispersal treatment consisted of a single dispersal event. This was paired with a high biomass dispersal treatment where mesocosms received twice the amount of biomass of dispersers as the low biomass treatment, which also occurred during a single dispersal event. The influence of the timing of dispersal was assessed using a third treatment where mesocosms received low biomass over two dispersal events, three weeks apart. Thus, the timing of dispersal treatment received the same total biomass of dispersers as the high biomass treatment but over a longer time period. Dispersal events occurred over a period of three weeks during July and August 2013. Mesocosms were sampled in July 2014 to examine the effects of the dispersal treatment.

Analyses

For simplicity, in years when two sampling dates occurred, the late season sampling date (July) was used for data analysis since plant biomass in the tanks was higher later in the season. Paired Wilcoxon signed rank tests were conducted to determine if drought impacted local community (mesocosm) species richness or regional treatment level species richness of 10 communities between 2011 and 2013 using R (R Core Development Team 2012). Changes in community composition between 2011 and 2013 in response to drought were analyzed with Raup-Crick pairwise dissimilarities in a Permutation-based ANOVA (PERMANOVA) using the *raupcrick* and *adonis* functions in the Vegan Package in R (Oksanen et al. 2010). Differences in species composition between these two years were visualized by creating a Nonmetric multidimensional scaling (NMDS) plot of the Raup-Crick dissimilarities using the PRIMER software package (Clarke and Gorley 2006).

A null species occupancy model was created in R to assess if species responses to the drought disturbance were non-random. This model follows the conceptual framework of a null model of random extinction created by Smith et al. (2009). The number of species that went extinct in each community between 2011 and 2013 was calculated and used as a constant in the model. In each run, the identity of species that went extinct in each of the 40 communities was chosen at random. The occupancy of each species in the 40 communities was calculated after each run and saved. The model was executed 1000 times and upper and lower 95% confidence intervals were determined for each species' expected occupancy post drought. Species' actual occupancies in 2013, after the drought, were compared to the null model expectation.

Plant trait data were analyzed to determine if species that experienced an increase in community occupancy after the drought have a different suite of traits than species that had a reduction in occupancy. The two algae species in this study were excluded from this analysis because of the lack of comparable trait data. A Gower dissimilarity matrix (Gower 1971) was calculated from plant traits (Table 3.1) of species that had a post drought occupancy that either increased or decreased compared to the null expectation using the *daisy* function of the cluster package in R (Maechler et al 2014). A PERMANOVA was conducted on this dissimilarity matrix to determine if species with differential responses to drought had a different composition of traits using the *adonis* function of the Vegan Package in R (Oksanen et al. 2010). The Gower dissimilarity index was chosen because it is ideal for plant traits since it can compute dissimilarities for data containing quantitative and qualitative traits (Laliberté and Legendre 2010).

Differences in community species richness and percent volume following dispersal were analyzed using a Kruskal-Wallis rank sum test comparing species richness between treatments in 2014. Post-hoc tests were conducted using the *postho.kruskal.nemenyi.test* function with Chi-squared approximation in the PMCMR package in R (Pohlert 2014). Raup-Crick pairwise dissimilarities were compared among communities of different dispersal treatments using PERMANOVA (Oksanen et al. 2010) to measure differences in species composition. Post-hoc PERMANOVA analyses were conducted comparing the differences in species composition between each dispersal treatment combination. Differences in species composition between the dispersal treatments were visualized by creating a NMDS plot of Raup-Crick dissimilarities (Clarke and Gorley 2006).

Paired Wilcoxon signed rank tests were conducted for each treatment comparing the species richness between pre drought (2011) and post dispersal (2014) conditions to determine if the dispersal treatments facilitated the recovery of community species richness to the pre drought conditions in 2011. Species composition of dispersal treatment communities was also compared to pre-drought conditions in 2011 to determine if species composition had returned to pre-drought conditions using a PERMANOVA on Raup-Crick dissimilarities with year and treatment as factors (Oksanen et al. 2010).

Results

In response to the historic drought in 2012, average local community species richness decreased between 2011 and 2013 from 7.35 to 5.48 species (Figure 3.1, Wilcoxon test, paired comparisons, $P < 0.001$). Average regional treatment level species richness of 10 communities also decreased between 2011 and 2013 from 13.75 to 10 species (Figure 3.1, Wilcoxon test, paired comparisons, $P = 0.098$). The whole experiment level species richness decreased as well from 16 to 11 species between 2011 and 2013 (Figure 3.1).

PERMANOVA on pairwise compositional differences showed that sampling year had a significant effect on species composition (Figure 3.2, $F = 21.839$, $P < 0.001$).

Communities were more compositionally similar in 2013, after the drought, and there was an overall shift in species composition between 2011 and 2013 (Figure 3.2). This shift in species composition was paired with changes in species' occupancies before and after the drought disturbance (Figure 3.3 and Table 3.1). Six species (37.5%) had higher community occupancies than expected after the drought, while five species (31.25%) had

lower occupancies, and five species had occupancies within the 95% confidence intervals. A PERMANOVA comparing the composition of traits between plant species that had higher community occupancy than expected after drought to those that had lower occupancy than expected was not significant ($P > 0.6$).

Average local community species richness in July 2014 varied among dispersal treatments (Figure 3.4, light grey bars, Kruskal-Wallis test, $P < 0.01$). This significant difference among treatments was due to differences between the species richness of the control communities and high dispersal ($P < 0.01$) and dispersal over time ($P < 0.05$) communities (Figure 3.4). There was no difference between the average percent volume of communities in different dispersal treatments. PERMANOVA on pairwise compositional differences between communities showed that dispersal treatment had a significant effect on species composition (Figure 3.5, $F = 2.604$, $P = 0.015$). Post-hoc PERMANOVA analyses comparing the differences in composition between individual dispersal treatments revealed that this difference is due to the control treatment being compositionally different from the three dispersal treatments (Table 3.2).

Paired Wilcoxon signed rank tests for each treatment comparing the species richness between pre drought (2011) and post dispersal (2014) revealed that the dispersal treatments facilitated the recovery of community species richness to the pre drought conditions in 2011 (Figure 3.4). There was no significant difference in the species richness of the three dispersal treatments between 2011 and 2014. However, the species richness of the control communities was lower in 2014 than 2011 (Wilcoxon test, paired comparisons, $P = 0.027$). A PERMANOVA on species composition of the three dispersal treatment communities in 2014 compared to their pre-drought conditions in

2011 showed that there was a main effect of sampling date ($F = 32.673$, $P = 0.001$), but not dispersal treatment ($F = 0.931$, $P = 0.51$), and there was no interaction between the sampling date and dispersal treatment ($F = 0.768$, $P = 0.768$). This indicates that dispersal treatment communities in 2014 were compositionally different from their pre-drought conditions in 2011.

Discussion

In response to a historic drought, local species richness of aquatic plant communities decreased and communities became more similar in their species composition. Aquatic plant species were lost from local communities, as well as the regional levels of treatment and the entire experiment (Figure 3.1). There was also a change in species composition between pre and post drought sampling dates (Figure 3.2). Species composition shifted between pre and post drought sampling dates, and communities became more similar to one another after the drought (Figure 3.2). A variety of disturbances in different ecological systems have been found to increase compositional similarity between communities (Chase 2007, Lepori and Malmqvist 2009, Smith et al 2009). A loss of species from the regional species pool and an increase in community similarity following a disturbance suggests that the disturbance selectively removed species from the community, however this pattern could occur from random extinctions, necessitating a null model approach to disentangle the relative influence of stochasticity and determinism (Chase 2007, Smith et al 2009, Chase and Myers 2011). The effect of drought on species in this experiment was highly selective as 68.75% of species had occupancy levels that were significantly influenced (positively or negatively) by drought (Figure 3.3). However, there was still an element of stochasticity in the response of

species to the drought, as some low occupancy species went extinct, which was within the null model expectation (Figure 3.3).

Drought was a selective disturbance for many of the species in this experiment, so plant traits were measured to test whether the change in species' occupancies following drought. However, for this experiment, the effect of drought on species' responses to disturbance cannot be explained using their traits. The plants used in this study represent a wide range in growth forms and morphologies (Table 3.1). In another similar study of over 50 species of aquatic plants in 59 shallow lakes, Arthaud et al. (2011) found that functional diversity did not vary according to disturbance frequency. The lack of significance in this study is not unexpected based on the geographic distributions and evolutionary history of these species. Functional traits can show geographic distributions strongly correlated with climate (Swenson and Weiser 2010), and aquatic plants in general have broad geographic distributions (Santamaria 2002). All of the species in this study have geographic distributions that at least cover the lower 48 states of the United States of America (USDA, NRCS 2014), suggesting that they have traits necessary to survive in a wide array of climates. Proposed explanations for the broad distributions of aquatic plants include clonal growth and reproduction, which increases their tolerance to stress, as well as the generality of broad plastic responses, which are promoted by traits such as clonal growth and the high amount of temporal variability aquatic plants experience (Santamaria 2002).

Dispersal treatments differentially affected community richness. Species richness was significantly greater in the high biomass and high biomass over time dispersal treatments as compared to the control (Figure 3.4). Furthermore, species richness in the

low biomass treatment was intermediate to the control and high biomass treatments (Figure 3.4). The species richness in all three dispersal treatments recovered to their pre drought species richness (Figure 3.4), suggesting that even low amounts of species dispersal can facilitate the recovery of species richness.

The dispersal treatments also reduced the similarity among communities when compared to control communities (Figure 3.5). Although there was a recovery of species richness with increased dispersal and a decrease in community similarity, there were still differences in species composition between pre-drought and post-drought and dispersal communities. This difference in species composition is to be expected, since in dynamic systems it is difficult for any measure to return to an exact prior state in time (Palmer et al. 1997, Jentsch 2007).

Recovery from disturbance is not entirely dependent on propagule dispersal from outside sources. Aquatic plants can persist in seed banks (Matthews et al. 2009), although several studies of wetland restoration have concluded that seed banks are a poor source of propagules (Brown 1998, Wetzel et al. 2001). In the present study, it appears as though seed banks may play a role in the recovery of species richness over long time periods. There were eight instances of species reappearing in control tanks that received no dispersal two years following the drought. Since aquatic plants are dispersal limited when not connected via direct waterways or animal dispersal (Capers et al. 2010, Akasaka and Takamura 2012), the species that reappeared in control tanks most likely came from a seed bank or other storage organs.

In this study I found that local community richness decreased and community similarity increased following a severe drought disturbance. In this system, recovery of

species richness and dissimilarity among communities was facilitated by additional dispersal into disturbed communities. In natural systems, species dispersal is dependent upon the availability of propagules as well as mechanisms of dispersal. Since aquatic plants are dispersal limited, having a nearby source to disperse from is critical. In a study of wetland restoration, it is suggested that many species colonize from within tens of meters of a target site (Ashworth et al. 2006). The small amount of dispersal required for the recovery of species richness in this experiment implies that having a small refugium for aquatic plants subjected to a landscape-wide disturbance may provide the potential for species dispersal, and facilitate the eventual recovery of aquatic plant communities.

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Table 3.1: Table of species traits compiled from lab measurements, Whitley et al. (1999), and Arthaud et al. (2012). Post Drought Occupancy describes the change in a species' occupancy of experimental communities following the drought in 2012 relative to the null expectation. Asterisk (*) denotes an invasive species inadvertently introduced into one community.

Species	Group	Family	Morphology	Longevity	Fecundity	Leaf Area (cm ²)	SLA	Post Drought Occupancy
<i>Elodea canadensis</i>	Monocot	Hydrocharitaceae	SC	Pr	Mv	0.57	178.82	no change
<i>Myriophyllum spicatum</i>	Dicot	Haloragaceae	TC	Pr	Mv	0.79	124.01	no change
<i>Sagittaria latifolia</i>	Monocot	Alismataceae	MR	Pr	Hv	92.28	44.56	no change
<i>Spirodela polyrrhiza</i>	Monocot	Lemnaceae	FF	Ar	Hv	0.78	74.67	no change
<i>Lemna minor</i>	Monocot	Lemnaceae	FF	Ar	Hv	0.36	108.05	decrease
<i>Najas flexilis</i>	Monocot	Najadaceae	MC	A	M	0.47	134.08	decrease
<i>Polygonum hydropiperoides</i>	Dicot	Polygonaceae	TF	Pr	Mv	8.26	44.93	decrease
<i>Ceratophyllum demersum</i>	Dicot	Ceratophyllaceae	FF	Pr	Mv	1.20	92.83	increase
<i>Nymphaea odorata</i>	Dicot	Nymphaeaceae	TF	Pr	Mv	342.03	28.11	increase
<i>Potamogeton nodosus</i>	Monocot	Potamogetonaceae	TF	Pr	Hv	15.69	49.31	increase
<i>Potamogeton pusillus</i>	Monocot	Potamogetonaceae	SC	Ar	Hv	0.89	174.75	increase
<i>Potamogeton diversifolius</i>	Monocot	Potamogetonaceae	TF	Pr	Hv	-	-	no change
<i>Potamogeton zosteriformis</i>	Monocot	Potamogetonaceae	SC	Ar	Hv	-	-	decrease
<i>Eleocharis acicularis</i>	Monocot	Cyperaceae	SR	P	Mv	-	-	decrease
<i>Spirogyra</i>	Green Algae	Zygnemataceae	-	-	-	-	-	increase
<i>Oedogonium</i>	Green Algae	Oedogoniaceae	-	-	-	-	-	increase

Morphology: SR small rosette, MR medium rosette, SC small caulescent, MC medium caulescent, TC tall caulescent, FF free floating, TF tall floating, Longevity: Pr perennial with storage organs, P perennial without storage organ, Ar annual with storage organ, A annual without storage organ, Fecundity: Hv high number of reproductive organs, seed and vegetative propagules, H high number of reproductive organs only seed, Mv medium number of reproductive organs, seed and vegetative propagules, M medium number of reproductive organs, only seed

Table 3.2: Results of post-hoc PERMANOVA analyses comparing the differences in composition between individual dispersal treatments using Raup-Crick dissimilarities.

Treatment	Control	Dispersal 1	Dispersal 2
Dispersal 1	F = 3.193 P = 0.057		
Dispersal 2	F = 6.553 P = 0.003	F = 1.378 P = 0.317	
Dispersal Time	F = 4.315 P = 0.013	F = -0.104 P = 0.878	F = 1.003 P = 0.444

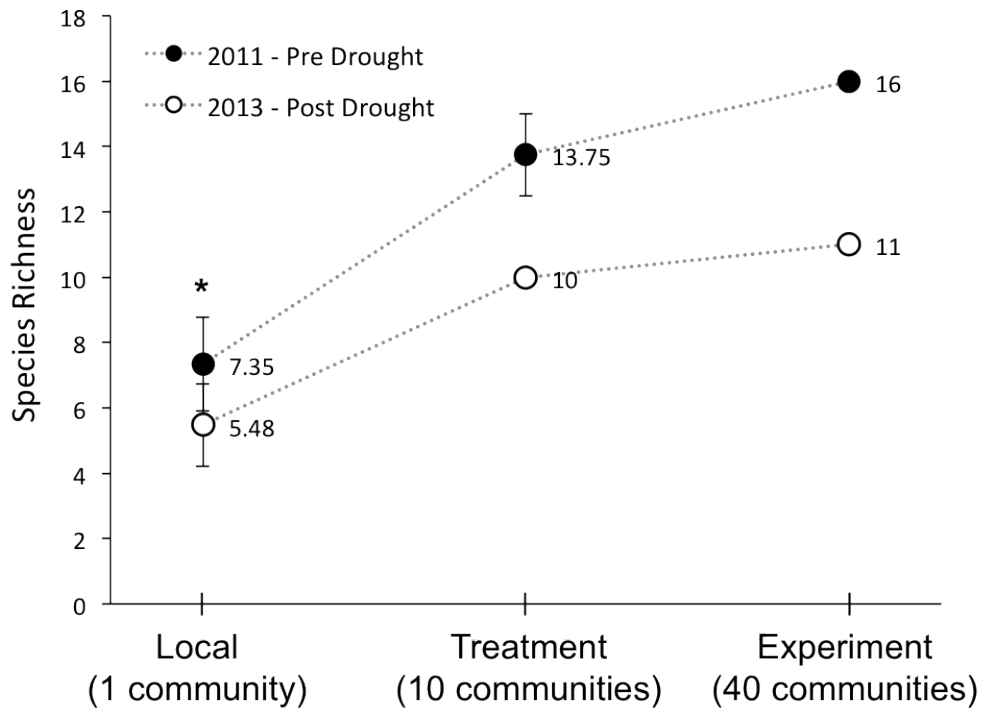


Figure 3.1: Effects of drought disturbance on species richness (\pm SD) at the local (1 community), treatment (4 replicates of 10 communities), and experiment (40 communities) level. Black circles represent species richness in 2011 before the drought disturbance, and white circles denote species richness in 2013 after the drought. Asterisk (*) indicates a significant difference ($P < 0.05$) in species richness between years determined via a paired Wilcoxon signed rank test.

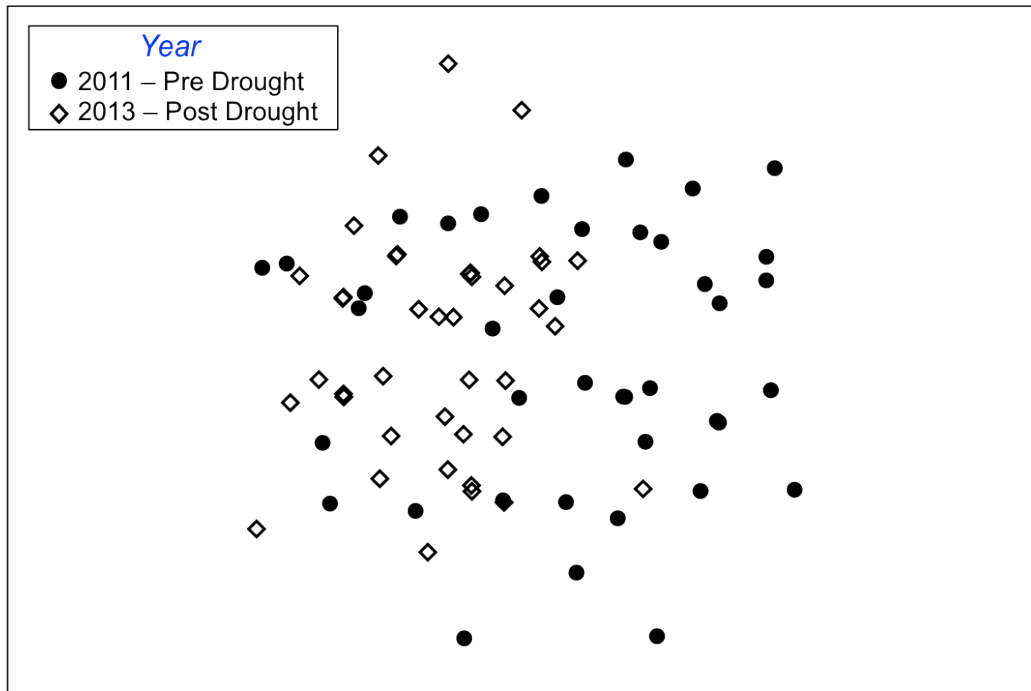


Figure 3.2: Nonmetric multidimensional scaling (NMDS) of aquatic plant communities in two-dimensional space using species presence/absences data. Each point represents an experimental community, and the distance between any two points represents the difference in Raup-Crick dissimilarity between those two communities. The black circles represent data from 2011, before the drought, while the white diamonds are communities in 2013, after the drought. Community composition is significantly different between 2011 and 2013 (PERMANOVA, $F = 21.839$, $P < 0.001$).

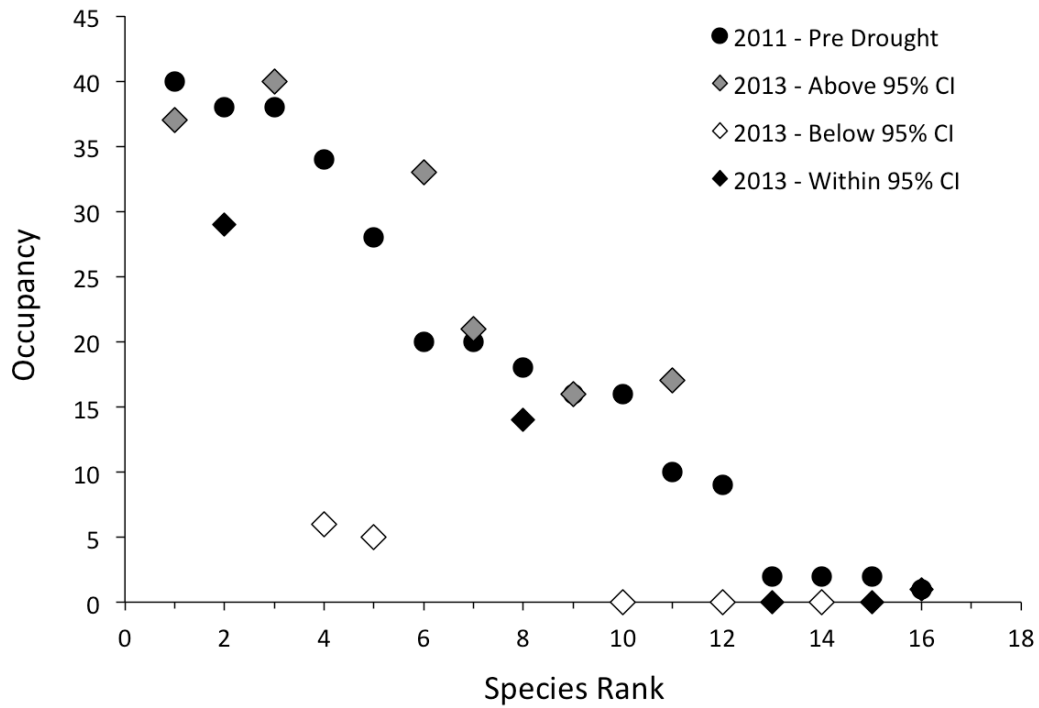


Figure 3.3: Change in species occupancy following drought (but before dispersal) relative to the null model expectation. The black circles represent the species rank occupancy distribution in 2011 before the drought. The diamonds denote species occupancy in 2013, the year after the drought. Grey diamonds are species whose occupancy increased above the null expectation, white diamonds denote species with occupancies below the null expectation, and black diamonds are species that fall within the null expectation for occupancy following the drought.

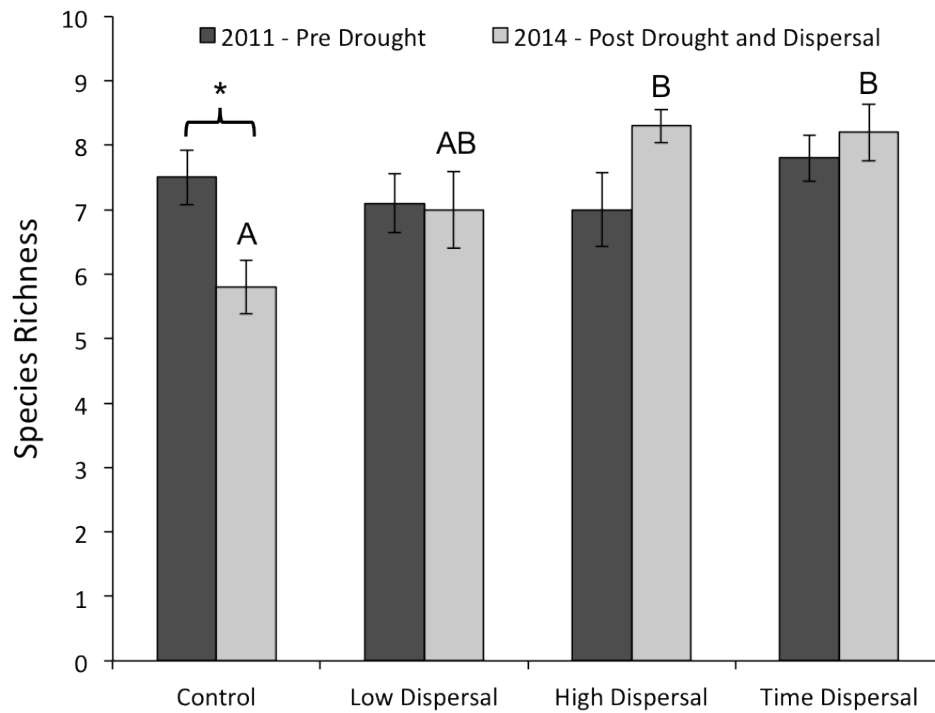


Figure 3.4: Light grey bars represent the effect of dispersal treatment on average community species richness (\pm SE) in 2014 (Kruskal-Wallis test, $P < 0.01$). Treatments marked with different letters are significantly different from one another. Dark grey bars depict average community species richness in 2011, before the drought. Paired Wilcoxon signed rank tests were conducted for each treatment to compare community species richness between pre drought (2011) and post dispersal (2014) conditions. Treatments with a significant difference ($P < 0.05$) in species richness between the two dates are denoted by an asterisk (*).

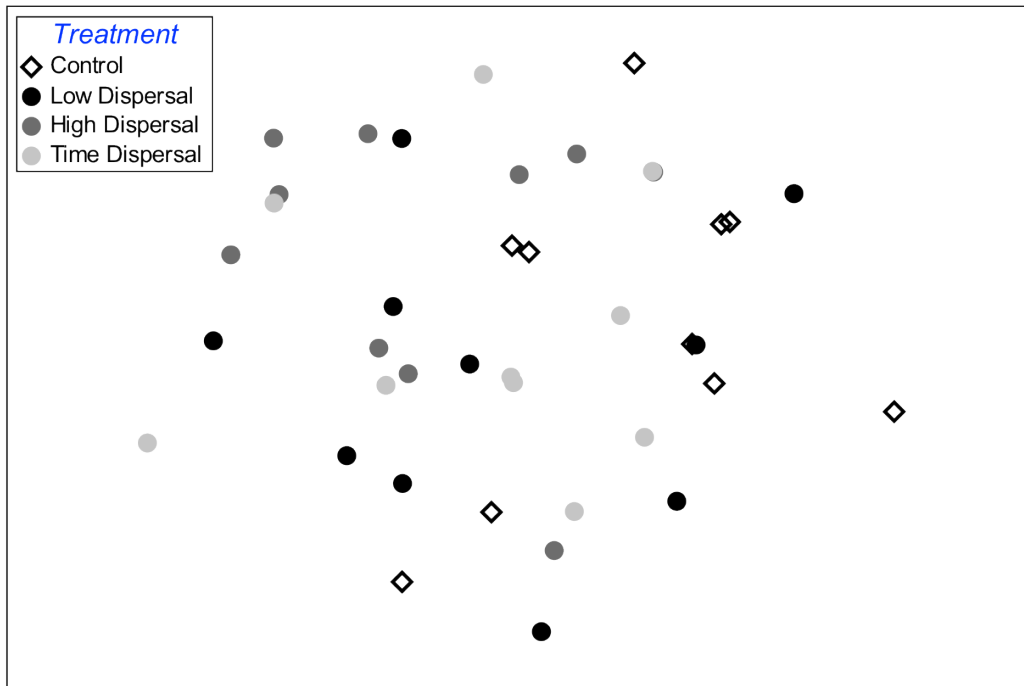


Figure 3.5: Nonmetric multidimensional scaling (NMDS) of aquatic plant communities in 2014, post drought and dispersal treatment, in two-dimensional space. Each point represents an experimental community, and the distance between any two points represents the difference in Raup-Crick dissimilarity between those two communities. The white diamonds represent communities in the control treatment, while the different shaded circles denote communities in the different dispersal treatments.

Dissertation Conclusions

The overall goal of this research was to examine the influence of metacommunity size and landscape-level processes, such as dispersal, on species diversity. Through a combination of theory, field surveys, and experiments, I found that metacommunity size can influence species richness at local and regional spatial scales, and that dispersal can influence the recovery and maintenance of species richness.

Using a theoretical model, I found that the effect of metacommunity size, and thus habitat destruction, on species richness depends on whether species immigration rates or extinction rates are more affected by metacommunity size. When immigration rates increase with metacommunity size, z decreases with metacommunity size. This is because the higher immigration rates in large metacommunities cause patches to be more similar in species composition, and thus have lower turnover in species between small and large patches when compared to small metacommunities. When extinction rates decrease with metacommunity size, z increases with metacommunity size, and there is higher turnover in species composition between small and large patches within a large metacommunity than within a small metacommunity. The changes in z values in this model are a result of differential effects of metacommunity size on small versus large patch species richness, which has important implications for predicting species loss following habitat destruction in fragmented landscapes. If metacommunity size alters immigration rates, species loss following habitat destruction via a reduction in metacommunity size will be greater in small patches relative to large patches. Conversely, if metacommunity size alters extinction rates, then habitat destruction will have little effect on the species richness of small patches within a metacommunity, but result in a more severe loss in species richness in large patches.

In Chapter 2, I examined the effect of metacommunity size on species richness at local and regional spatial scales using a field survey of zooplankton species in replicate pond metacommunities. I found that metacommunity size has scale-dependent effects on zooplankton species richness. As the number of ponds in a metacommunity increase, the species richness of local ponds increases, but there is no change in richness at the regional spatial scale due to decreases in the turnover of species among communities. These results match the theoretical predictions for the effect of increased dispersal rates on local and regional species richness as well as species turnover. Additionally, I found an increase in species evenness at the metacommunity level as metacommunity size increases. In this study system, metacommunity evenness appears to be increased in large metacommunities through a reduction in the abundance of the most common species, which was typically one of two copepod species from the family *Cyclopidae*, *Microcyclops rubellus* or *Mesocyclops edax*. The results of this study are similar to those of other studies examining the effects of metacommunity size on species richness patterns, and they provide one of the first examples of species richness patterns changing with metacommunity size in a non-experimental system.

In Chapter 3, I conducted an experiment investigating the effect of a natural drought disturbance on species richness in aquatic plant communities, and the importance of dispersal for the recovery of species richness. I found that local species richness decreased in response to drought, and communities became more similar in their species composition. The overall effect of drought on plant species in this experiment was highly selective as 68% of species had community occupancies after the drought that were either higher or lower than expected by chance, implying that species were lost as a result of

deterministic processes. Since drought was a selective disturbance for many of the species in this experiment, plant traits were measured to see if they could explain the change in species' occupancies following drought. However, the effect of drought on species' occupancies was not explained by functional traits.

Increasing species dispersal after the drought disturbance promoted the recovery of species richness. Species richness in all three dispersal treatments recovered to their pre-drought conditions, suggesting that even low amounts of species dispersal can facilitate the recovery of species richness in aquatic plant communities. The dispersal treatments also increased the dissimilarity among communities when compared to control communities. However, there were still differences in species composition between pre-drought and post-drought dispersal communities. In natural systems, species dispersal is dependent upon the availability of propagules as well as mechanisms of dispersal. Since aquatic plants are dispersal limited, having a nearby source to disperse from is critical. Thus, the recovery of species richness following a disturbance in natural aquatic plant communities will likely depend on the metacommunity context.

This dissertation demonstrates that metacommunity size can affect species richness patterns. However, the effect of metacommunity size on species richness patterns will likely depend on the dispersal ability and life history characteristics of the organisms considered. For instance, passive dispersers such as zooplankton, may be more likely to have their immigration rates affected by metacommunity size, while active dispersers might be more likely to be affected by extinction effects since they might preferentially select some habitats over others within a metacommunity, ultimately lowering the extinction rate in that particular patch through the rescue effect. I also found that

dispersal was important for the recovery of species richness following a drought disturbance in aquatic plant communities. If metacommunity size alters species dispersal in natural systems, which this research suggests, then metacommunity size could influence the recovery and maintenance of species richness in disturbed systems through promoting species dispersal. A broader understanding of how habitat destruction and disturbance will influence metacommunity species richness requires considering the landscape context, including the size of the metacommunity.